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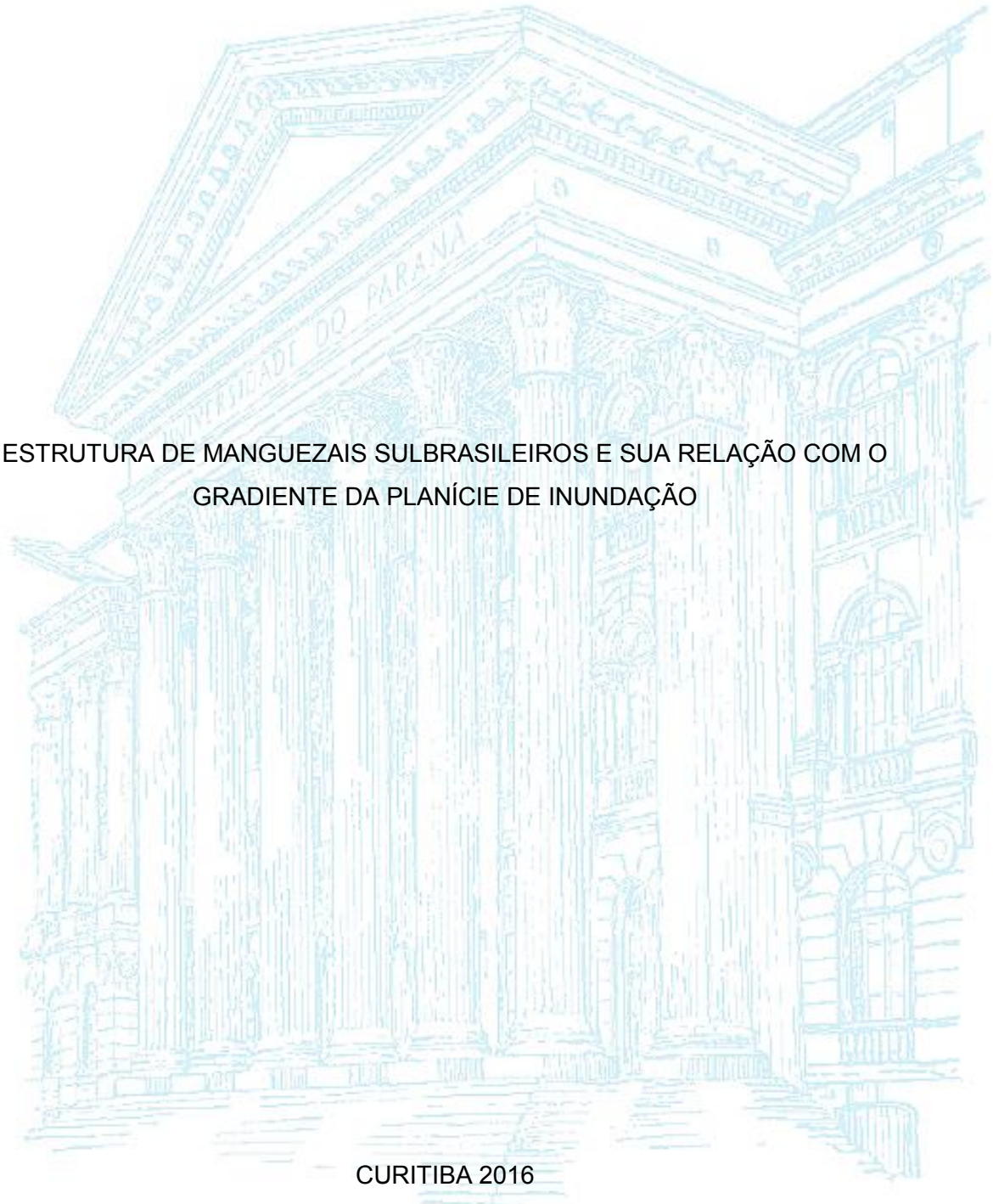

ESTRUTURA DE MANGUEZAIS SULBRASILEIROS E SUA RELAÇÃO COM O GRADIENTE DA PLANÍCIE DE INUNDAÇÃO

CURITIBA 2016

LETICIA LARCHER DE CARVALHO

ESTRUTURA DE MANGUEZAIS SULBRASILEIROS E SUA RELAÇÃO COM O GRADIENTE DA PLANÍCIE DE INUNDAÇÃO

Tese apresentada como requisito parcial à obtenção do grau de Doutora em Ecologia e Conservação ao Curso de Pós-Graduação em Ecologia e Conservação da Universidade Federal do Paraná.

Orientadora: Dra. Maria Regina Torres Boeger

Co-Orientadores: Prof. Dr. André A. Padial (UFPR) e Prof. Dr. Leonel Sternberg (University of Miami).

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PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da tese, a que se submeteu **Letícia Larcher de Carvalho** para fins de adquirir o título de Doutora em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão do candidato.

Secretaria do Programa de Pós-Graduação em Ecologia e Conservação.

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“What on Earth is this unlike?
Which plant is forming a living dyke?
Who is rooting in the sea?
The mangrove tree,
The mangrove tree.”
(Farid Dahdouh-Guebas)

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RESUMO

Manguezais são ecossistemas costeiros que representam a área de transição entre os ambientes marinhos e terrestres. As espécies arbóreas que ocorrem neste ecossistema apresentam adaptações para lidar com fatores que variam amplamente nos manguezais, como salinidade do solo e dinâmica hidrológica. Apesar dos esforços em descrever a estrutura dos manguezais, investigações que abordem os processos ecológicos ainda são necessárias para o estabelecimento de medidas de conservação dos manguezais, baseado na variedade de respostas às alterações ambientais em diferentes escalas. Estudos sugerem que a distribuição das espécies e estrutura dos manguezais florestas são influenciadas por diferenças ecológicas entre as espécies, como tolerância à concentração de nutrientes no solo e à salinidade. Entretanto, as espécies estão sujeitas à fatores que variam em diferentes escalas (global, regional e local). Este estudo teve como objetivo avaliar a ecofisiologia das espécies e sua relação com o ambiente e variações em diferentes escalas, através de três abordagens: 1) A estrutura de manguezais sulbrasileiros e a relação entre o padrão de distribuição das espécies e fatores ambientais que variam em escala local; 2) O padrão de distribuição das espécies como resultado da influência das variações ambientais locais na ecofisiologia das espécies; 3) A eficácia dos levantamentos de estrutura existentes nos manguezais ao longo da costa brasileira em estimar os padrões regionais na estrutura e a relação entre as variáveis ambientais e a estrutura destes manguezais. Portanto, o primeiro capítulo desta tese avaliou a distribuição das espécies arbóreas de manguezais subtropicais geograficamente próximos. De forma complementar, o segundo capítulo desta tese avaliou a relação entre a distribuição das espécies e fatores ambientais que variam em escala local, como composição e textura do sedimento. Parâmetros fitossociológicos da vegetação arbórea de três manguezais foram avaliados comparativamente: Estuário do Rio Nhundiaquara (Baia de Antonina, PR), Estuário do Rio Pinheiros (Baía de Guaratuba, PR) e Estuário do Rio Palmital (Baia da Babitonga, SC). *Rhizophora mangle* L. (Rhyzophoraceae), *Avicennia schaueriana* Stapf & Leechm. ex Moldenke. (Acanthaceae), e *Laguncularia racemosa* (L.) Gaertn. (Combretaceae) ocorreram nas áreas estudadas, porém com diferenças estruturais. Essas diferenças podem ser atribuídas à aspectos geográficos em escala local e na exigência das espécies à disponibilidade de nutrientes, como por exemplo, *Rhizophora mangle* e *L. Racemosa,* que diferiram na tolerância aos teores de Ca e P no solo, resultando distribuição distintas entre baías. Para avaliar os limites de tolerância das espécies e o gradiente ambiental natural na planície de inundação, no

terceiro capítulo, foram analisados parâmetros de trocas gasosas e a abundância de isótopos estáveis de Carbono ($\delta^{13}C$) e Nitrogênio ($\delta^{15}N$), em parcelas ao longo gradiente de inundação do estuário do Rio Pinheiros, em que as espécies apresentam zonação. *Avicennia schaueriana* mostrou a capacidade de manter alta eficiência intrínseca do uso da água (WUEi), mesmo sob alta salinidade. O $\delta^{13}C$ foliar de *L. racemosa* foi menor do que as outras espécies e negativamente relacionado com a salinidade da água intersticial, o que pode explicar o padrão de distribuição das espécies. Os parâmetros de trocas gasosas de *R. mangle* não foram correlacionados com as variáveis ambientais. Os indivíduos de borda tedem à usar uma fonte marinha de N, ao contrario de manguezais mais internos, embora a diferença não seja significativa para *R. mangle*. A forma como espécies respondem às mudanças na salinidade da água intersticial pode ser observada tanto nos parâmetros de troca de gás, quanto na assinatura isotópica das espécies, definindo o padrão de zonação encontrado. O quarto capítulo compilou levantamentos fitossociológicos em áreas de manguezais, de 2000 à 2015, afim de responder as seguintes questões: os levantamentos representam padrões regionais na estrutura dos manguezais ao longo da costa brasileira? Ainda, os dados existentes são suficientes para estabelecer a relação entre as variáveis ambientais e a estrutura destes manguezais? Apesar de caracterizar a estrutura das comunidades ao longo da costa brasileira, os estudos não definiram os processos que influenciam a estrutura de cada manguezal. A investigação de componentes específicos, como respostas a variações nos fatores abióticos e bióticos, pode elucidar os processos que resultaram nos padrões estruturais atualmente encontrados.

Palavras-chave: ecofisiologia de manguezal; fitossociologia; salinidade; eficiência do uso da água; assinatura isotópica; isótopos estáveis.

ABSTRACT

Mangroves are coastal ecosystems that represent the transition between marine and terrestrial environments. Tree species that occur in this ecosystem are able to deal with factors that vary widely in the mangroves, such as soil salinity and hydrological dynamics. Despite efforts to describe the structure of mangroves, investigations that address the ecological processes are still needed for establish mangrove conservation measures, based on the variety of specific responses to environmental changes at different scales. Previous studies suggest that distribution and structure of mangrove forests are influenced by ecological differences among species, such as tolerance to soil nutrients concentration and soil salinity. However, species are subject to factors that vary at different scales (global, regional and local). This study aimed to evaluate physiological ecology of species and its relationship with environment variations at different scales using three approaches: 1) the structure of mangroves and the correlation between pattern of species distribution and environmental factors that vary in local scale; 2) The distribution pattern of species as a result of the influence of local environmental variations in species ecophysiology; 3) The effectiveness of the structure surveys in mangroves along the Brazilian coast to estimate regional structural patterns and the relationship between environmental variables and the structure of these mangroves. The first chapter of this thesis characterizes the structure of three subtropical mangroves. The second chapter correlates species distribution to environmental conditions. Mangroves of the Antonina Bay (PR), Guaratuba Bay (PR) and the Babitonga Bay (SC) were analyzed. *Rhizophora mangle* L. (Rhyzophoraceae), *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (Acanthaceae) and *Laguncularia racemosa* (L.) Gaertn. (Combretaceae) occurred in the areas studied. Each studied mangrove presented a pattern of species distribution linked to differences in physicochemical factors along the floodplain gradient and the degree of tolerance that each species presents. Nutrient availability constrains species distribution, e.g. *R. mangle*, and *L. racemosa* differed in tolerance to nutrient concentrations in the soil, such as calcium and phosphorus. Our results indicate the significance of the distance from the coast, showing the weight of factors that vary in a local scale. In the third chapter, we measured gas exchange rates and the isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) of three mangrove species in plots along an inundation gradient, to investigate if photosynthetic capacity and water use efficiency constrain distribution and development of mangrove in the Guaratuba Bay. *Avicennia schaueriana* showed the capacity to maintain high *WUEi,* even with high g_s under higher salinities. The foliar

$\delta^{13}C$ of *L. racemosa* was lower than the other species and negatively correlated to pore-water salinity, which may explain the species distribution pattern. The parameters of gas exchange in *R. mangle* did not correlate to the measured soil variables. The results indicate that fringe mangroves may use a marine source of ^{15}N, although the difference was not significant to *R. mangle*. How species respond to changes in pore-water salinity is expressed in both gas exchange parameters and isotopic signature through the salinity gradient, which indicates that zonation may be related to species ecophysiological responses to salinity variations. The fourth chapter reviewed phytossociological surveys in mangrove areas from 2000 to 2015 in order to answer the following questions: 1. Do the existing data represent regional patterns in the structure of mangroves along the Brazilian coast? 2. Are the data available sufficient to establish the relationship between environmental variables and structure of these mangroves? The studies have not defined the processes that influence the structure of each mangrove although they characterize the structure along the Brazilian coast. The investigation of variations in responses to abiotic and biotic factors may elucidate the processes that resulted in the structural patterns observed today.

Key-Words: mangrove ecophysiology; forest structure; salinity; water use efficiency; isotopic signature; stable isotopes.

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INTRODUÇÃO

Os manguezais correspondem a um tipo de vegetação arbóreo-arbustiva, que se desenvolve ao longo da zona de influência das marés, tanto no interior do estuário, quanto na costa tropical e subtropical (Tomlinson 1986). Ocorrem sob solos ricos em nutrientes, com baixa concentração de oxigênio em decorrência da variações de marés, que impulsionam as águas salgadas do mar para dentro do continente através do canal fluvial e para as laterais dos rios em zonas sujeitas a inundações ao longo dos estuários (Hogarth and Hogarth 2007).

Com distribuição mundial, os manguezais ocorrem predominantemente na região entre os trópicos de Câncer e Capricórnio, apresentando maior desenvolvimento na região equatorial (Tomlinson 1986). A área de cobertura estimada para comunidades de manguezal varia entre 10 e 18 milhões de hectares, entretanto, este número originalmente era muito superior (Kathiresan and Bingham 2001; Lüttge 2008; Spalding et al. 2010).

No Brasil, os manguezais ocorrem desde o extremo norte (Oiapoque 04°30'N) no Amapá até Santa Catarina (Laguna 28°30'S), correspondendo a 6800 km, aproximadamente (Schaeffer-Novelli et al. 1990). Apesar de o sudeste asiático ter a maior área de cobertura de manguezal, cerca de 33,5% da cobertura mundial, a maior área contínua desse ecossistema encontra-se na região Nordeste da costa brasileira, representando 4,3% dos mangues no mundo (Spalding et al. 2010). Devido à sua importância ecológica, no Brasil, existem esforços para a manutenção e conservação dos manguezais através de leis que protegem esses ecossistemas como Áreas de Proteção Permanente (Lei Federal nº 12.651/2012 - Código Florestal). Entretanto, ainda há intensa atividade humana interferindo na conservação de áreas de manguezais. Atividades antrópicas são constantes nos manguezais, devido à conversão das áreas costeiras em outros usos, como por exemplo, aquicultura, desenvolvimento urbano e turístico, entre outros (Spalding et al. 2010).

A diversidade de espécies arbóreas ocorrentes nos manguezais é reduzida quando comparada com outras florestas tropicais (Schaeffer-Novelli et al. 1990; Dodd and Afzal Rafii 2001; Kathiresan and Bingham 2001). As poucas espécies ocorrentes compartilham a habilidade de resistirem às condições halofíticas das águas estuarinas ou regiões costeiras com influência de águas marinhas (Lüttge 2008), em constante inundação, com alta salinidade, e em substratos não consolidados com baixa oxigenação (Kathiresan and Bingham 2001; Hogarth and Hogarth 2007).

Cerca de 54 espécies em 20 gêneros, pertencentes a 16 famílias, formam a flora associada aos manguezais (Tomlinson 1986). Comumente, estas espécies são consideradas “exclusivas” de áreas entre marés e raramente são encontradas em outros ambientes, tendo sua distribuição influenciada pela temperatura e umidade relativa do ar (Duke 1993; Krauss et al. 2008). No Brasil, o ecossistema manguezal pode ser representado por uma associação de espécies dos gêneros *Rhizophora, Avicennia, Laguncularia* e *Conocarpus*. Com certa frequência, também ocorrem espécies dos gêneros *Hibiscus, Acrostichum* e *Spartina* (Schaeffer-Novelli and Cintrón-Molero 1986; Schaeffer-Novelli et al. 1990).

Apesar de apresentar baixa diversidade de espécies vegetais, os manguezais exibem variabilidade em suas características estruturais e funcionais (Lugo and Snedaker 1974; Tomlinson 1986; Lüttge 2008; Pascoalini et al. 2014). Ao longo da costa brasileira, a variedade de fatores ambientais influencia a ocorrência e o desenvolvimento destas espécies, resultando em manguezais estruturalmente diferentes (Schaeffer-Novelli et al. 1990; Dodd and Afzal Rafii 2001; Kathiresan and Bingham 2001).

Fatores abióticos, bióticos e antrópicos atuam em diferentes escalas espaciais e temporais. Salinidade, temperatura, radiação solar, precipitação, vento, aporte de água doce, nutrientes, dinâmica de marés e de ondas, competição interespecífica por recursos, predação, entre outros, podem ser citados como fatores que moldam a estrutura das florestas de manguezais (Lima and Tognella 2012). Estes atuam em diferentes níveis hierárquicos de organização espacial ou escalas (Krauss et al. 2008; Estrada et al. 2013). Em escala global, a temperatura é o principal fator que limita a distribuição das espécies de manguezal, sendo seu limite coincidente com a isoclina de 20º C (Lüttge 2008; Krauss et al. 2008). Em escala regional, o balanço entre precipitação, evapotranspiração e dinâmica de inundação das marés determina a disponibilidade de água no solo e limita o estabelecimento e desenvolvimento das espécies (Lugo and Snedaker 1974; Schaeffer-Novelli et al. 1990; Twilley and Day 2012).

Em escala local, a estrutura da floresta é principalmente controlada pela frequência de inundação, determinada pela topografia e aporte de água doce (Lugo and Snedaker 1974; Snedaker 1982; Estrada et al. 2013). Entretanto, fatores bióticos, como predação, utilização de recursos, competição entre indivíduos por espaço, luz, água e nutrientes também determinam o desenvolvimento destas comunidades e formam o complexo de fatores que, invariavelmente, são dependentes entre si (Lugo and Snedaker 1974; Schaeffer-Novelli et al. 1990; Twilley and Day 2012).

Desta forma, a distribuição espacial das espécies não pode ser explicada somente por um único fator ambiental, visto que pode haver interação entre fatores. Por exemplo, ao longo do gradiente de inundação, variações na tolerância à salinidade, mudanças temporais no solo, problemas de dispersão e de competição após a colonização inicial, além de outros fatores possivelmente ainda não percebidos, dificultariam a definição de um padrão de distribuição nítido das espécies (Lüttge 2008; Lima and Tognella 2012).

A expressão da sucessão vegetal em resposta às mudanças geomorfológicas e fisiológicas locais aos gradientes das marés é caracterizada como zonação (Snedaker 1982). Os processos que promovem a zonação interferem de forma diferenciada no estabelecimento de propágulos, plântulas, jovens e indivíduos adultos. O resultado é a distribuição das espécies, representando o processo de interação com o ambiente em todo o ciclo de vida dos indivíduos (Snedaker 1982; Hogarth and Hogarth 2007; Lüttge 2008). Como pode haver covariação e interação de alguns fatores ao longo do gradiente de inundação, os padrões de zonação diferem em escala local, regional e global (Lugo and Snedaker 1974; Snedaker 1982), de acordo com os fatores mais atuantes.

Características de solo estão entre os fatores ambientais mais importantes que afetam diretamente a produtividade e estrutura de manguezais. As propriedades físicas e químicas que mais afetam são o pH (concentração de íons de hidrogênio), Eh (potencial de redução) e tamanho das partículas do solo (Ball 1988; Ferreira et al. 2010; Madi et al. 2015). A tolerância à salinidade, no entanto, é reconhecida como o fator vital que regula o crescimento e distribuição das espécies de mangue (Ball 1988; Kathiresan and Bingham 2001; Parida and Jha 2010).

Os manguezais ao longo da costa do Oceano Atlântico no continente americano foram anteriormente definidos pela dominância de espécies dos gêneros *Avicennia* e *Laguncularia* em florestas de transição e pela dominância de *Rhizophora* em florestas marginais (Madi et al., n.d.; Schaeffer-Novelli et al., 2000; Sobrado, 2000; Lugo et al., 2007). No entanto, a dominância de espécies de mangue em zonas é controversa. Um conjunto de respostas fisiológicas são responsáveis pela distribuição das espécies: espécies de *Avicennia* estão associadas a áreas em que a evaporação excede a precipitação, devido à alta eficiência de uso da água (Medina and Francisco 1997; Sobrado and Ewe 2006a; Reef et al. 2010; Farquhar et al. 2014), enquanto as espécies *Rhizophor*a dominam solos menos salinos, em que a água doce é mais expressiva, devido à baixa tolerância a variações de salinidade (Lacerda 2009; Da Cruz et al. 2013). Espécies de *Laguncularia* foram relatadas em áreas protegidas ao longo dos canais e

banhada por águas doces, devido à baixa tolerância à salinidade (Sobrado 2005; Sobrado and Ewe 2006b; Lugo et al. 2007; Bartz et al. 2015).

A salinidade da água intersticial, contida entre as partículas de solo, é resultante da variação na frequência de inundação pelas marés e tem sido uma da variáveis mais analisadas, pois correlaciona-se estreitamente com a distribuição das espécies (Snedaker 1982; Lovelock et al. 2006a; Lüttge 2008). Sua variação é modulada pela dinâmica das águas salinas de origem marinha no manguezal, cuja amplitude determina a renovação das águas superficiais e intersticiais (Krauss et al. 2006; Ferreira et al. 2010; Bompy et al. 2014). Essa renovação tem papel importante na seleção e fixação de propágulos, bem como no transporte e distribuição de matéria orgânica particulada e/ou dissolvida (folhas, ramos, restos de animais) e oxigênio para as regiões adjacentes (Lovelock et al. 2006b; Feller et al. 2010; Reef et al. 2010).

Em geral, a salinidade afeta o desempenho das plantas pelo déficit de água, pela toxidez provocada por íons que geram desequilíbrio nutricional e, indiretamente, mediando competições interespecíficas (Ball 1988; Esteves and Suzuki 2008; Lüttge 2008). Em altas salinidades, a condutância estomática é reduzida (Lin and Sternberg 1992; Sobrado 2005; Lugo et al. 2007), o que acarreta menor perda de água, porém também reduz a entrada de CO_2, e consequentemente, o crescimento do indivíduo. O estresse salino afeta a eficiência fotossintética por acarretar baixa condutância estomática, que causa o decréscimo nas taxas de CO_2 acumulado e transpiração, e aumenta a tensão nos vasos do xilema (Sobrado and Ewe 2006b; Sobrado 2007; López-Portillo et al. 2014).

A eficiência fotossintética e a condutância estomática das folhas podem ser afetadas, tanto pelas variações momentâneas de salinidade quanto pela exposição a longo período em altas concentrações de salinidade (Ball 1996; Medina 1999; Lugo et al. 2007). Em decorrência destas condições, a demanda de água para compensar os gastos com a transpiração é variável. Geralmente, as taxas fotossintéticas dos manguezais têm o ponto de saturação em baixos níveis de luz, apesar de estarem presentes em ambientes com alta exposição solar (Lüttge 2008; Farquhar et al. 2014). No entanto, o requerimento de luz entre as espécies é variável.

Exclusão, tolerância e secreção de sal são alguns dos mecanismos ecofisiológicos presentes nas espécies de mangue, variando tanto entre espécies quanto para a mesma espécie em diferentes condições ambientais (Liang et al. 2008; Parida and Jha 2010; Krauss and Ball 2013). As diferentes estratégias espécie-específicas de tolerância à salinidade podem determinar a espécie

dominante no dossel. Entretanto, os manguezais apresentam heterogeneidade na estrutura dos bosques, não apenas relacionado com a ocorrência dos indivíduos, mas também com as características estruturais e funcionais, como resultado da variação local dos fatores ambientais.

De acordo com Schaeffer-Novelli et al. (1990), a costa brasileira pode ser dividida em sete unidades de mapeamento, em que a fisiografia é semelhante e a estrutura de florestas de mangue tende à variar entre as unidades. No entanto, a estrutura dos manguezais é variável mesmo dentro de cada unidade (Souza et al., 1996; Sessegolo, 1997; Silva et al., 2005; Matni et al., 2006; Estrada et al., 2013).

A Região Sul é de ampla importância para o entendimento da ecologia dos manguezais por ser o limite de ocorrência desse ecossistema (Soares et al. 2003; Soares et al. 2012; Estrada et al. 2013; Soares et al. 2015). Nos manguezais sul-brasileiros são encontradas três espécies vegetais: *Rhizophora mangle* L. (Rhyzophoraceae), *Avicennia schaeuriana* Stapf & Leechm. ex Moldenke (Acanthaceae), e *Laguncularia racemosa* (L.) Gaertn. (Combretaceae) (Schaeffer-Novelli et al. 1990). Apesar de sua importância, não há registros de estudos em escala regional que permitam a visualização dos padrões de estrutura nos manguezais sul brasileiros.

Em muitas áreas do litoral sul brasileiro, as características da costa levam à substituição dos manguezais por vegetação de marismas (Oliveira and Tognella 2014), porém, o fator que exerce maior influencia na ocorrência desses manguezais é a temperatura. Os limites de latitude para a distribuição de mangues provavelmente são determinados pela ocorrência de baixas temperaturas durante o inverno. Entretanto, estudos sobre a ecofisiologia dos manguezais em seu limite sul de distribuição na costa do Oceano Atlântico são escassos e insuficientes para elucidar as particularidades dos processos que levam à ocorrência e à distribuição das espécies (Soares et al 2015, Falqueto et al 2008, Mehlig et al 2010).

Os levantamentos encontrados na Região Sul são restritos a três principais sistemas: Baia de Paranaguá (PR), Baia de Babitonga (SC) e Ilha de Santa Catarina (SC). A Baia da Babitonga (SC) abriga a maior extensão de áreas de manguezal do litoral sulbrasileiro, enquanto outras áreas do litoral abrigam bosques com menor expressividade em termos de extensão, mas importantes na contribuição da qualidade ambiental costeira. Os estudos nesta região são escassos e sugerem não haver um padrão de distribuição que abrange todos os manguezais (Dornelles et al. 2006; Kilca et al. 2011; Soares et al. 2012; Soares et al. 2015; Madi et al. 2016).

A Baia de Paranaguá, no entanto, tem sido alvo de levantamentos de manguezal desde 1946 (Sessegolo 1997; Bigarella 2001; Madi et al. 2016). Apesar

de ser um sistema de pequena extensão, os resultados são divergentes quanto a ocorrência de zonação nos manguezais, em parte, por serem de épocas diferentes. No entanto, esses autores são unânimes em afirmar sobre a influência da salinidade na densidade e distribuição dessas espécies vegetais.

Ainda no litoral paranaense, a Baia de Guaratuba é o segundo maior complexo estuarino, com 48,72 km^2. Embora sua importância para a aquicultura do Estado do Paraná, não há muitos estudos sobre os manguezais de seus estuários. Apesar de ainda não apresentarem alto grau de degradação, já existem registros de pressões causadas pela expansão urbana nos manguezais sulbrasileiros, por exemplo, em decorrência da construção de portos e pela indústria de lazer (Lana et al. 2001; Angulo et al. 2006; Vieira et al. 2008).

A busca pelos padrões de distribuição das espécies nos manguezais é relatada desde os primeiros estudos ecossistêmicos, afim de identificar quais os processos e variáveis atuantes nesta configuração (Pool et al. 1977; Cintron and Novelli 1984; Cintrón and Schaeffer-Novelli 1985; Li and Lee 1997; Bigarella 2001). Comparar a estrutura dos manguezais é complexo, devido à variedade de componentes influenciando a ocorrência e distribuição das espécies, por exemplo, as configurações geológicas e hidrológicas da área estudada (Krauss et al. 2008). Apesar dos esforços em descrever a estrutura, investigações que abordem os processos ecológicos de manguezais ainda são necessárias para o estabelecimento de medidas de manejo e sustentabilidade de áreas costeiras, baseado na variedade de respostas às alterações ambientais em diferentes escalas (local, regional e global) e sua importância ecológica para os ambientes costeiros (Soares 1999; Hogarth and Hogarth 2007; Godoy and Lacerda 2015).

Portanto, este estudo, dividido em três capítulos, teve como objetivo investigar a estrutura e a ecofisiologia das espécies de manguezais sulbrasileiros, além de avaliar se os levantamentos existentes representam padrões regionais na estrutura dos manguezais ao longo da costa brasileira.

O primeiro artigo que compõe a tese está intitulado “Mangrove forest structure and species distribution pattern in Southern Brazil” e encontra-se em fase de preparação para submissão ao periódico Brazilian Archives of Biology and Technology. Tem como objetivo caracterizar a estrutura de três manguezais subtropicais e sua relação com condições ambientais, para verificar se espécies arbóreas de manguezais seguem um padrão de distribuição em manguezais subtropicais e se esse padrão é modulado por variações nas variáveis ambientais locais

O segundo artigo que compõe a tese, intitulado “Linking subtropical Brazilian mangrove forest structure to local environmental attributes and species preferences” está sob avaliação no Brazilian Journal of Botany. Este artigo teve como objetivo investigar a estrutura e os padrões de distribuição das espécies de manguezais sul-brasileiros e relacionar a ocorrência das espécies com as variações ambientais, em escala local, em que ocorrem.

O terceiro artigo, intitulado “Are gas exchange adjustments in order to cope with soil features affecting mangrove zonation in Southern Brazil?” está sob avaliação no periódico Aquatic Botany. Este artigo teve como objetivo avaliar se as respostas ecofisiológicas das espécies, como padrões de trocas gasosas e assinatura isotópica, estão relacionadas com o padrão de zonação encontrado e as variações ambientais locais relativas ao gradiente da planície de inundação.

O quarto artigo, intitulado “Uma revisão sobre manguezais no Brasil: a relação entre estrutura de floresta e variações ambientais” teve como objetivo compilar diversos estudos sobre estrutura e fitossociologia de manguezais, para avaliar se os levantamentos existentes representam padrões regionais na estrutura dos manguezais ao longo da costa brasileira, e se são suficientes para estabelecer a relação variáveis ambientais/estrutura de manguezais. Esse capítulo encontra-se em fase de tradução para posterior submissão ao periódico Natureza e Conservação.

CAPÍTULO 1

MANGROVE FOREST STRUCTURE AND SPECIES DISTRIBUTION PATTERN IN SOUTHERN BRAZIL

Mangrove forest structure and species distribution pattern in Southern Brazil

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Abstract

Aims: This study characterizes the structure of three subtropical mangroves and correlates it to environmental conditions to verify (1) if tree species follow a distribution pattern in subtropical mangroves and (2) if it is modulated by variations in local environmental variables.

Methods: Fifteen 50 m^2 plots parallel to the river were demarcated in fringe (5), intermediary (5), and transition (5) mangrove areas along three subtropical estuaries of Southeastern Brazil: Antonina, Guaratuba, and Babitonga Bays. In each plot, we analyzed soil features, forest structure, and tree species distribution.

Results: Rhizophora mangle L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, and *Laguncularia racemosa* (L.) Gaertn. occur in the studied estuaries and display different distribution patterns. Local differences in particle size and pore water salinity were correlated to species distribution. Differences indicate that mangrove structure is related to species plasticity and tolerance.

Conclusions: Mangrove structure was related to a set of environmental variables that varies geographically and to species tolerance environmental changes. Species physiognomy and forest structure are a result of pressures at different scales, as the distance from the coast, sediment features and salinity.

Keywords: phytosociology; mangrove gradients; ecological zonation.

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Introduction

Mangroves represent a transition ecosystem between marine and terrestrial environments (Schaeffer-Novelli 1995). They can be found from 04º30'N to 28º30'S, under an extensive range of environmental settings (Schaeffer-Novelli et al. 1990). In this ecosystem, factors vary resulting in a heterogeneous environment, such as tides, salinity, wind, temperatures, irradiance, and flood, sediments nutrient concentrations (Ball 2002; Hogarth 2007). The heterogeneity of environment requires specific morphological and physiological strategies from mangrove tree species (Schaeffer-Novelli 1995; Medina 1999; Bernini and Rezende 2004) to cope and survive in the particular environmental conditions of mangroves (Lüttge 2007).

Interactions between forest species and the environment where they grow can determine both the spatial and temporal patterns in the structural composition of mangrove forests (Scheffer-Novelli 1999). Spatial species distribution cannot be explained by a single environmental factor (Cintrón and Schaeffer-Novelli 1985; Dodd and Afzal Rafii 2001; Kathiresan and Bingham 2001; Bernini and Rezende 2004). Patterns of structure and distribution in mangroves have been reported since the first studies, in effort to explain the ecological processes that resulted in current configurations (Lugo and Snedaker 1974; Cintrón and Schaeffer-Novelli 1985; Sessegolo 1997; Bigarella 2001, among others). The consequence of the species range of tolerance levels to the covariance of environmental factors can be a variety of zonation patterns (Tomlinson 1986).

Mangrove forests occur along the Brazilian coast, from northernmost (Amapá State) to the southern region (Santa Catarina State) (Schaeffer-Novelli et al., 2000), which represents the southernmost occurrence of mangroves in the Atlantic West Coast. Five tree species occur along the Brazilian coast, however, only three species are found in subtropical mangroves: *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (Acanthaceae), and *Laguncularia racemosa* (L.) Gaertn. (Combretaceae). Despite the importance of subtropical mangroves, there are no studies on a regional scale that allow the visualization of forest structure patterns. Despite some patterns have been found, there is a wide variation in forest structure, even among mangroves that are geographically close, revealing the ecosystem complexity (Sessegolo 1997; Bigarella 2001; Cunha et al. 2006; Dornelles et al. 2006; Kilca et al. 2011).

Many studies support the influence of abiotic variables on the density and distribution of mangrove tree species, although, especially in subtropical mangroves, the scale of influence may vary along the floodplain gradient, due to salinity or other factors such as soil texture and nutritional composition. Changes in soil physical-chemical attributes, e.g. from

sandy to clayey, were considered important to define the distribution of species in mangrove forests at Babitonga Bay, Santa Catarina State, Brazil (Kilca et al. 2011). Substrate composition, especially organic matter contents and salinity, also influence the distribution of species in subtropical mangroves at Paranaguá Bay (Paraná State, Brazil), mainly the density of *A. schaueriana* and the density and dominance of *L. racemosa* and *R. mangle* (Martins et al. 2016). Also, tide dynamics and particle size of substrate may have an additional effect on species distribution (Sessegolo 1997).

Thus, this study aimed to characterize the structure of three subtropical mangroves and correlate it to environmental factors. In order to evaluate the influence of environmental variation on the distribution of tree species in these areas, the following points were assessed: (1) the characterization of structure and species pattern of distribution along the floodplain within each mangrove, (2) the influence of sediment particle size distribution and sediment nutrient composition on mangrove tree structure.

Methods

Study area

This study was conducted in three estuaries in southern Brazil: Antonina Bay, Guaratuba Bay and Babitonga Bay (Table 1, Fig 1):

Table 1-1 Location and environmental parameters of the studied mangroves at Antonina, Guaratuba, and Babitonga Bays.

	Antonina bay	Babitonga bay	Guaratuba bay
Location	Nhundiaquara River Estuary	Palmital River Estuary	Pinheiros River Estuary
Climate	Humid subtropical Cfa	Humid subtropical Cfa	Humid subtropical Cfa
Mean annual temperature (2012)	20.5□C	20.3□C	20.8□C
Annual rainfall (2012)	2733mm	2000mm	3183mm
Soil classification (EMBRAPA 2001)	Saline sodic Thiomorphic Gleysol	Saline sodic Thiomorphic Gleysol	Saline sodic Thiomorphic Gleysol

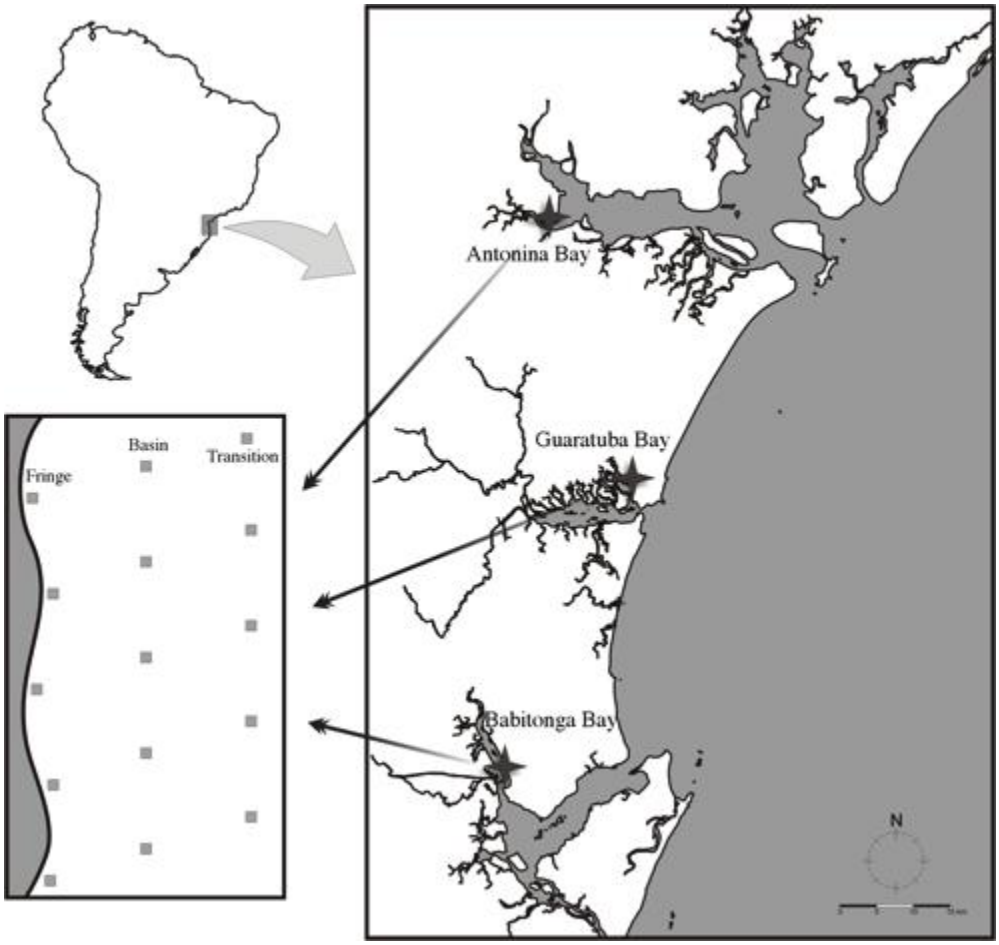

Figure 1-1: Location of studied sites and arrangement of plots in the estuaries of Antonina (A), Babitonga (B), and Guaratuba (G) Bays. Fringe plot; Basin : Intermediary plot; Transition plot.

Antonina Bay: the Estuary of Nhundiaquara River is located in the inner portion of the Antonina Bay (Brazil, 25º29'S - 25º28'S and 48º41'W - 48º44'W). Is microtidal bay, under a semi-diurnal tides regime directed by the reflux tides, and consists in the innermost bay along the current Brazilian coastline about 35 kilometers inside (Lana et al. 2001). The average temperature is 20.5°C, with 16.7°C and 26.4°C minimum and maximum values, respectively. The annual precipitation is 2773 mm (Meteorological System of State of Parana/SIMPEPAR).

Guaratuba Bay: the Estuary of Pinheiros River is located close to the mouth of the Guaratuba Bay (Brazil, 25º50'S - 25º48'S and 48º34'W - 48º36'W), approximately 4 kilometers away from the coastline. This bay is also classified as microtidal, ruled by semi-diurnal tides regime, with changes in amplitude due to potential storm floods events linked to high winds (Marone et al. 2005). The average annual rainfall is around 3183 mm and the

average temperature is 14.5°C in the winter season and 29.6°C in the summer (Meteorological System of State of Parana/SIMPEPAR). There is a marked saline stratification, increased in neap tide and low discharge of fresh water in the system (Marone et al. 2005).

Babitonga Bay: the Estuary of Palmital River is located in the middle portion of the Babitonga Bay (Brazil, 26º12'S - 26º06'S and 48º45'W - 48º47'W), about 20 kilometers away from the coastline. The average temperature is 16.5ºC in the winter season and 25.9ºC in the summer (Bartz et al. 2015). The annual rainfall is around 2265 mm (Agricultural Research and Rural Extension of the State of Santa Catarina/EPAGRI). The estuary is described as microtidal, ruled by semi-diurnal tides regime (Vieira et al. 2008).

Fifteen 50 m^2 plots parallel to the river were established along each estuary to characterize mangrove structures (Fig. 1). Plots were allocated at different distances from the water body based on field observations, in order to represent the floodplain gradient. They were classified into physiographic types: five fringe plots, representing the section close to the river; five intermediary plots; and five transitional plots, representing the section of transition between mangrove and Lowland Rainforests.

Abiotic factors

Salinity of pore water was measured at low tide with a digital hydrometer (Akso AK83) in five randomly selected points within each plot. 75 samples were obtained per bay. Soil texture was measured in one sample in each plot, 30 cm deep.

Vegetation Structure

In each plot, we measured the diameter at breast height (DBH, cm) and height (m) of all individuals at least 1.30 m high. Height was estimated with a hypsometer and DBH with a diameter tape. Absolute density (DA), relative density (DR), absolute frequency (FA), relative frequency (FA), absolute dominance (DOA), and relative dominance (DOR) were calculated according to Mueller-Dombois and Ellenberg (1974).

Data analysis

Means (± standard deviation) were calculated for all quantitative variables. Forest structure was tested with a PCA, using the densities of each species and of dead trunks within each plot as variables. Analyses were performed using the software "R" (R Development Core Team, 2009) with the "vegan" package (Oksanen et al. 2007) and "labdsv" (Roberts and Roberts 2007). Values were considered significant at $p \leq 0.05$.

Results

Abiotic factors

There were no variations in pore water salinity among plots within estuaries (ANOVA, Antonina: F: 2.09, p = 0.13; Guaratuba: F: 2.87, p = 0.06; Babitonga: F: 2.67, p = 0.07; n = 25), but values differed among estuaries: Guaratuba presents higher pore water salinity, followed by Antonina and Babitonga (ANOVA, F: 210.6, p <0.0001, n = 225) (Table 2). Particle-size distribution analysis showed that there was a predominance of silty-clay participles in Antonina bay, silty-frank in Guaratuba bay and silty-clay to sandy-clay in Babitonga bay (Table 2).

Table 1-2: Mean values (± standard deviation) of pore water salinity (‰), organic matter content (OM, 10 cm deep, $g.dm^{-3}$), Phosphorus content (P, 10 cm deep, $g.dm^{-3}$) and particle-size content (clay, silt, and sand, %) from sediments at Antonina bay, Guaratuba bay (Paraná, Brazil), and Babitonga bay (Santa Catarina, Brazil).

Plots	Pore water salinity (‰)	OM ($g.dm^{-3}$)	P ($g.dm^{-3}$)	Clay ($g.kg^{-1}$)	Silt ($g.kg^{-1}$)	Sand ($g.kg^{-1}$)
	Antonina bay					
Fringe	16.8 ±3.8	75.8 ±11.8	30.2 ±15.7	41.2 ±11	47.2 ±13	11.6 ±23
Intermediary	15.9 ±3.7	89.8 ±6.0	12.6 ±6.6	31.2 ±6	45.0 ±17	23.8 ±23
Transition	18 ±3.2	89.0 ±5.4	9.0 ±1	27.5 ±7	51.6 ±17	20.9 ±24
	Babitonga bay					
Fringe	9.6 ±4.6	75.2 ±18.5	16.8 ±6.9	37.0 ±15	32.4 ±16	30.6 ±7
Intermediary	8 ±4.8	87.2 ±10.2	18.2 ±3.6	52.0 ±21	17.5 ±3	30.5 ±22
Transition	6.8 ±3.9	85.8 ±12.8	9.3 ±3.2	27.1 ±27	12.7 ±6	60.2 ±21
	Guaratuba bay					
Fringe	22.4 ±2.8	73.8 ±8.7	12.8 ±2.7	26.1 ±14	36.7 ±11	37.2 ±24
Intermediary	19.8 ±3.4	58.5 ±19.1	9.5 ±3.9	22.2 ±11	33.0 ±7	44.8 ±14
Transition	20.9 ±4.4	71.5 ±16.1	13.5 ±6.7	26.3 ±21	29.7 ±17	44.0 ±13

PCA was performed using attributes soil texture as vectors. Sediment attributes explained 98.3% of the total variance. Soil texture attributes summarized most of data variance (Fig. 2). The first axis (PCA1) explained 68.7% of data variance and was mainly represented by sand content (eigenvector -0.80), clay content (eigenvector 0.41), and silt content (eigenvector 0.40). The second axis (PCA2) summarized 28.5% of data variance, mainly represented by silt (eigenvector 0.71) and clay content (eigenvector -0.70). A pattern related to area distribution emerged despite overlapping distribution. At Antonina bay, fringe plots were disconnected from basin and transition areas, especially for PCA2. Babitonga bay mangroves showed a distinct distribution in both PCAs, indicating that plots have different particle size content. At Guaratuba bay, fringe, basin, and transition plots had a greater variation in PCA1, especially for sand content.

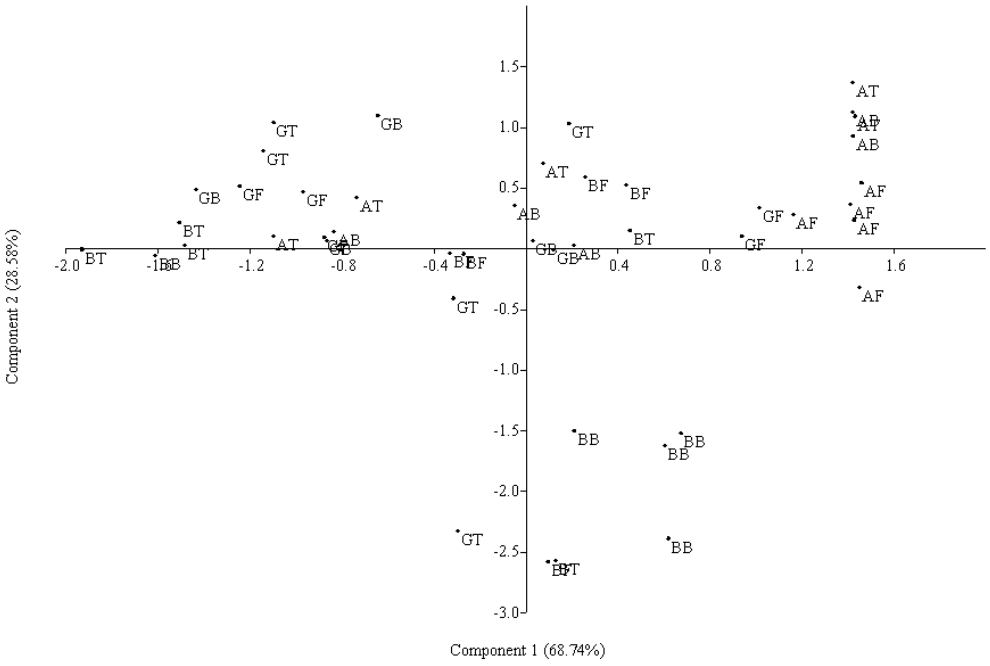

Figure 1-2 PCA of sediment parameters of mangroves at Antonina, Babitonga, and Guaratuba bays. Only the first two components are interpretable by the "Broken Stick" criterion. The percentage of each component is shown in the graphic. AF: Fringe Antonina Bay plots; AB: Intermediary Antonina Bay plots; AT: Transition Antonina Bay Plots; BF: Fringe Babitonga Bay Plots; BB: Intermediary Babitonga Bay Plots; BT: Transition Babitonga Bay Plots; GF: Fringe Guaratuba Bay Plots; GB: Intermediary Guaratuba Bay Plots; GT: Transition Guaratuba Bay Plots;

Vegetation structure

Avicennia schaueriana, R. mangle, and *L. racemosa* occurred in all studied mangroves. In Antonina Bay, we counted 277 individuals, among which 16 *A. schaueriana*, 49 *L. racemosa*, and 197 *R. mangle*, in addition to 15 dead trunks. In Guaratuba Bay, we surveyed 209 individuals, including 21 *A. schaueriana*, 84 *L. racemosa*, 90 *R. mangle*, and 13 dead trunks. At Babitonga Bay, we counted 154 individuals, including 25 *A. schaueriana*, 88 *L. racemosa*, and 34 *R. mangle*, and 7 dead trunks. Dead trunks were found in all areas, presented a higher coverage values (CV) and importance value (IV) in Guaratuba Bay. The mangrove species showed a wide variation in density, dominance, and frequency among bays and along the floodplain gradient.

At Antonina Bay, species were 6 to 9 m high and had a DBH between 9 and 12 cm (Fig. 3). Species showed differences among areas along the floodplain gradient. In fringe forests, *A. schaueriana* presented higher individuals with larger DBH. *Rhizophora mangle* individuals were higher in intermediary plots. In transitions plots, *L. racemosa* presented taller individuals and *R. mangle* had larger DBH (Table 3). *Rhizophora mangle* had the highest density, frequency, CV and IV in all plots. *Avicennia schaueriana* showed higher dominance values in fringe plots (Table 3), due to the presence of individuals with DBH larger than 30 cm.

Table 1-3: Mangrove vegetation structure in the Nhundiaquara River estuary, Antonina bay, Paraná, Brazil. Values are shown by floodplain gradient (fringe, basin and transition) and species (*Avicennia schaueriana*, *Laguncularia racemosa*, and *Rhizophora mangle*). Height mean values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation), AD: Absolute density (nº ind.ha^{-1}), ADo: Dominance of basal area (g.ha^{-1}), AF: absolute frequency (%), CV: Coverage value, IV: Importance value.

	A. schaueriana	*L. racemos*a	*R. mangle*	Dead Trunks
	Height (m)			
Fringe	10.8±4.4	6.6±1.6	8.7±1.7	5.0±0.6
Basin	5.1	6.3±1.9	7.9±1.6	7.1±1.7
Transition	-	6.5±1.9	6.3±1.1	5.0±0.6
	DBH (cm)			
Fringe	69.5±62.8	32.4±15.1	46.4±26.3	26.3±7.5
Basin	11.14	9.6±3.6	8.6±3.4	8.9±1.5
Transition	-	9.0±2.9	7.3±1.9	10.7±1.4
	AD (nº ind.ha^{-1})			
Fringe	500	799	1499	100
Basin	40	560	2840	320
Transition	-	550	4050	200
	ADo (g.ha-1)			
Fringe	34	8	34	0.8
Basin	0	4	19	1.2
Transition	-	4	18	2
	AF (%)			
Fringe	0.8	0.8	1	0.3
Basin	0.2	0.8	1	0.6
Transition	-	1	1	0.7
	CV			
Fringe	61.8	38	95.8	4.5
Basin	2.7	32.4	151.7	13.3
Transition	-	28.1	159.4	12.5
	IV			
Fringe	85.3	67.5	131.1	16.3
Basin	10.3	63.1	190.2	36.3
Transition	-	64.5	195.7	39.8

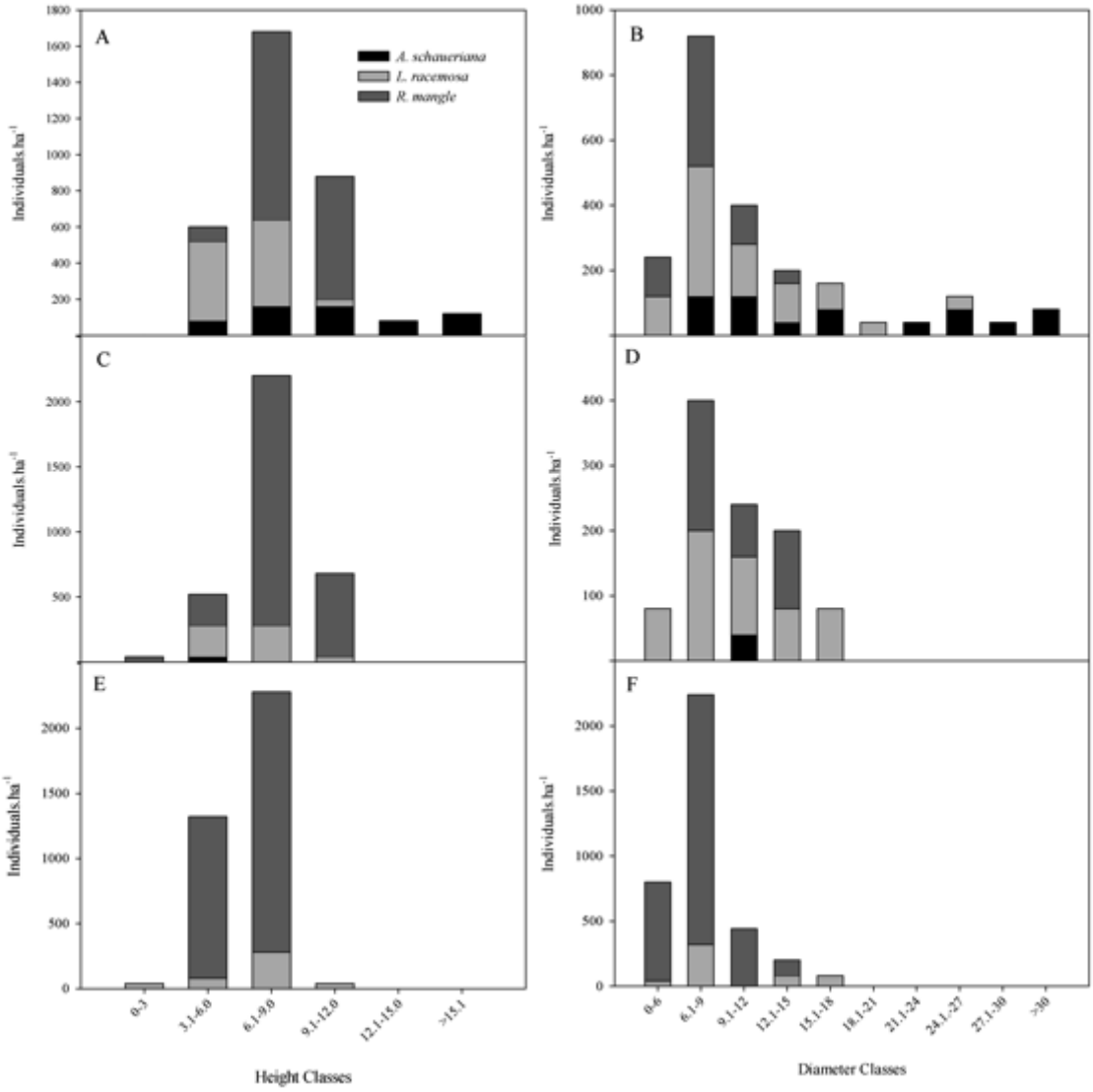

Figure 1-3: Distribution of live individuals by height and diameter classes in the mangrove community of Antonina Bay Estuary. A, B: Fringe Plots; C, D: Basin Plots; E, F: Transition Plots.

At Babitonga Bay, species exhibited larger average DBH (9 to 18 cm) than in Antonina and Guaratuba Bays, with individuals distributed in all diameter classes. Species were between 3 and 6 m high in fringe and transition plots and between 3 and 9 m in intermediary plots (Fig. 4). *Avicennia schaueriana* presented taller individuals in intermediary and transition plots. In fringe plots, *L. racemosa* individuals showed a higher average height. *Laguncularia racemosa* also presented a larger DBH in all studied plots. We found no differences among plots regarding structural parameters. *Laguncularia racemosa* exhibited higher density, dominance, frequency, CV and IV (Table 4).

Table 1-4: Mangrove vegetation structure in the Palmital River estuary, Babitonga bay, Santa Catarina, Brazil. Values are shown by floodplain zone (fringe, middle and inner zones) and species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*). Height means values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation), AD: Absolute density (nº ind.ha^{-1}), ADo: Dominance of basal area (g.ha^{-1}), AF: absolute frequency (%), CV: Coverage value, IV: Importance value.

	A. schaueriana	*L. racemos*a	*R. mangle*	Dead Trunks
	Height (m)			
Fringe	7.6±2.5	7.9±1.3	5.7±1.4	5.8±0.8
Basin	6.3±2.5	6.1±1.4	5.3±1.3	4.1±0.6
Transition	5.3±0.6	4.9±1.5	3.6±1.0	5.1±0.4
	DBH (cm)			
Fringe	16.5±12.4	20.9±16.4	7.9±2.0	8.1±1.0
Basin	14.6±8.3	18.4±13.1	10.0±2.7	11.0±2.0
Transition	18.7±11.7	20.5±13.4	9.2±3.0	16.2±7.2
	AD (nº ind.ha^{-1})			
Fringe	400	1166	566	100
Basin	360	1120	400	80
Transition	200	1250	350	100
	ADo (g.ha-1)			
Fringe	13	64	3	1
Basin	8	44	3	1
Transition	7	8	2	3
	AF (%)			
Fringe	1	1	1	0.5
Basin	1	1	0.8	0.4
Transition	0.5	1	0.5	0.5
	CV			
Fringe	34	131.6	29.1	5.3
Basin	32	136.3	26.2	5.5
Transition	46.4	106.8	28.7	18.1
	IV			
Fringe	61.8	159.4	56.9	22
Basin	63.3	167.5	51.2	18
Transition	66.4	146.8	48.7	38.1

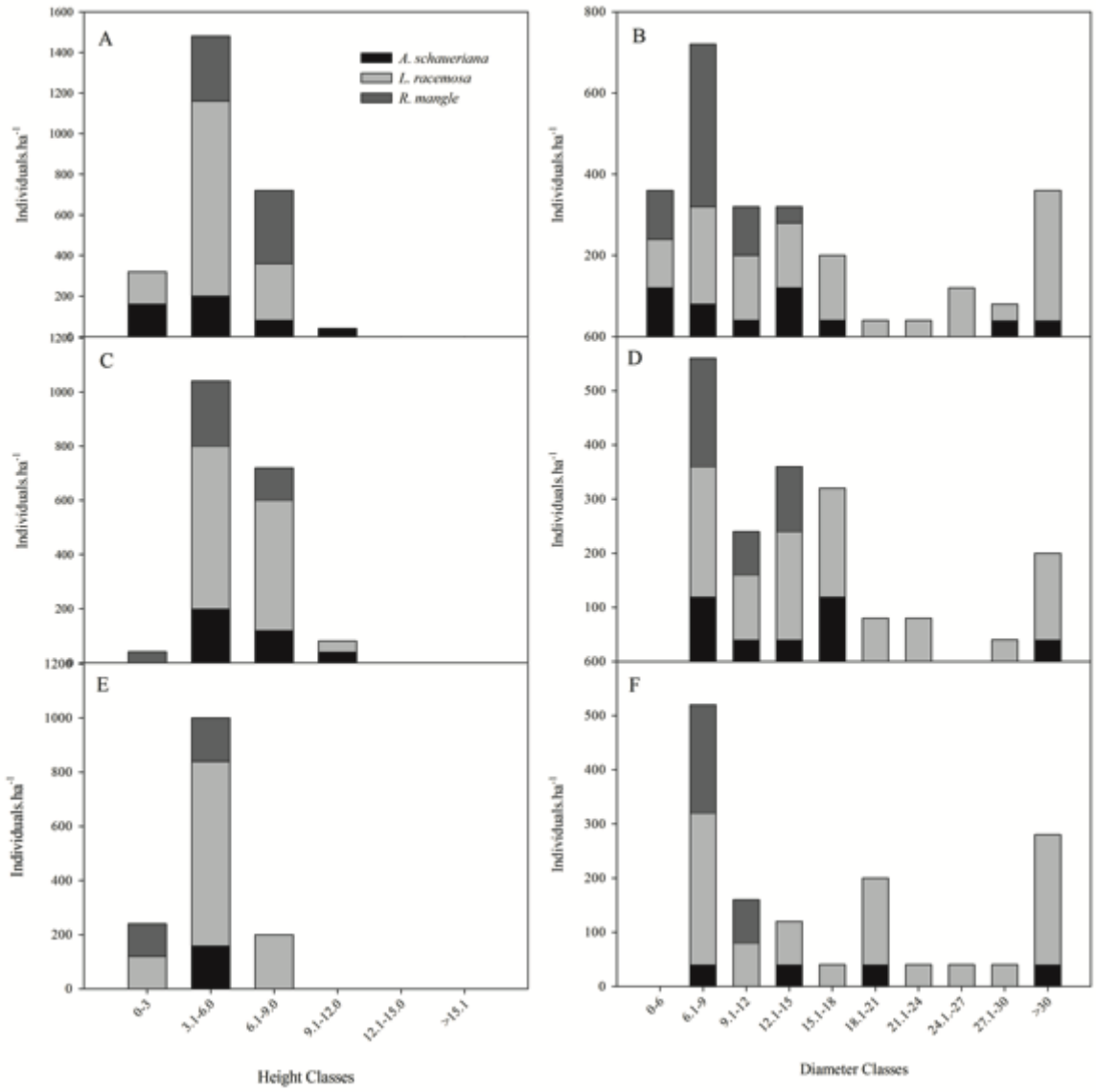

Figure 1-4: Distribution of live individuals by height and diameter classes in the mangrove community of Babitonga Bay estuary. A, B: Fringe Plots; C, D: Basin Plots; E, F: Transition Plots.

At Guaratuba bay, most individuals had a DBH between 6 and 12 cm and height varied from 3 to 6 m (Fig. 5). *Avicennia schaueriana* showed higher individuals and larger average DBH (Table 5). Species distribution presented a zonation pattern. In fringe plots, *L. racemosa* showed higher density, dominance, frequency, CV and IV. In intermediary plots, *L. racemosa* and *R. mangle* exhibited similar structure and distribution. In transition areas, *R. mangle* had higher density, dominance, frequency, CV and IV.

Table 1-5: Mangrove vegetation structure in the Pinheiros River estuary, Guaratuba bay, Paraná, Brazil. Values are shown by floodplain gradient (fringe, basin and transition) and species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*). Height means values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation), AD: Absolute density (nº ind.ha^{-1}), ADo: Dominance of basal area (g.ha^{-1}), AF: absolute frequency (%), CV: Coverage value, IV: Importance value.

	A. schaueriana	*L. racemos*a	*R. mangle*	Dead Trunks
	Height (m)			
Fringe	8.3±3.1	4.2±1.6	5.0±0.3	5.4±1.1
Basin	4.7±0.6	4.4±1.4	4.1±1.0	4.2±1.3
Transition	6.4±1.8	3.2±0.6	4.1±0.9	4.2±0.8
	DBH (cm)			
Fringe	26.0±11.1	14.6±11.5	15.5±3.3	9.8±2.3
Basin	14.8±7.0	8.9±4.2	8.8±2.8	6.0±0.5
Transition	21.5±13.7	13.9±6.2	8.9±5.6	6.6±2.4
	AD (nº ind.ha^{-1})			
Fringe	400	1360	120	200
Basin	200	1400	1480	160
Transition	240	600	2040	160
	ADo (g.ha-1)			
Fringe	25	36	2	2
Basin	4	11	10	0
Transition	12	11	18	1
	AF (%)			
Fringe	0.8	1	0.6	0.6
Basin	0.6	1	0.8	0.4
Transition	0.8	0.8	1	0.4
	CV			
Fringe	57.3	121.2	9.5	12.1
Basin	22	86.1	85.4	6.5
Transition	36.3	46.2	110.2	7.2
	IV			
Fringe	83.9	154.5	29.5	32.1
Basin	43.5	121.8	113.9	20.8
Transition	56.3	66.2	150.2	27.2

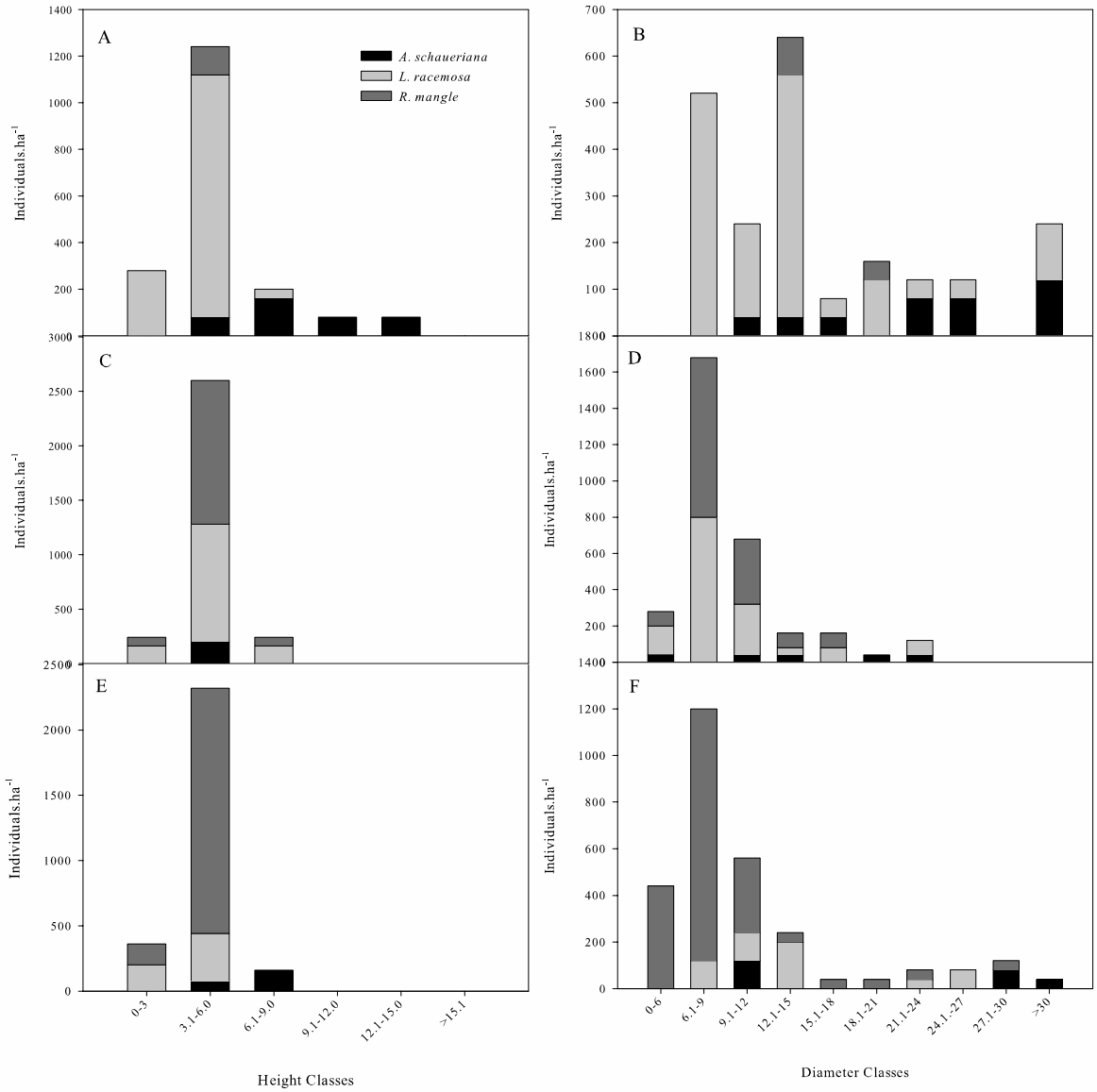

Figure 1-5: Distribution of live individuals by height and diameter classes in the mangrove community of Guaratuba Bay estuary. A, B: Fringe Plots; C, D: Basin Plots; E, F: Transition Plots.

The PCA using density of species and dead trunks in each plot explained 96.3% of total variance within mangroves (Fig. 6). *Laguncularia racemosa* and *R. mangle* densities seem to explain areas distribution better than *A. schaueriana* and dead trunks densities. The first axis (PCA1) explained 76.5% of data variance and is mainly represented by *R. mangle* (eigenvector -0.78) and *L. racemosa* (eigenvector 0.60) densities. The second axis (PCA2) summarized 19.8% of data variance and is mainly represented by *A. schaueriana* (eigenvector - 0.72) and *L. racemosa* (eigenvector 0.60) densities. The studied plots showed

overlapping in PCA1 and less variability in PCA2. Plots at Antonina bay presented less variation than at Babitonga and Guaratuba bays.

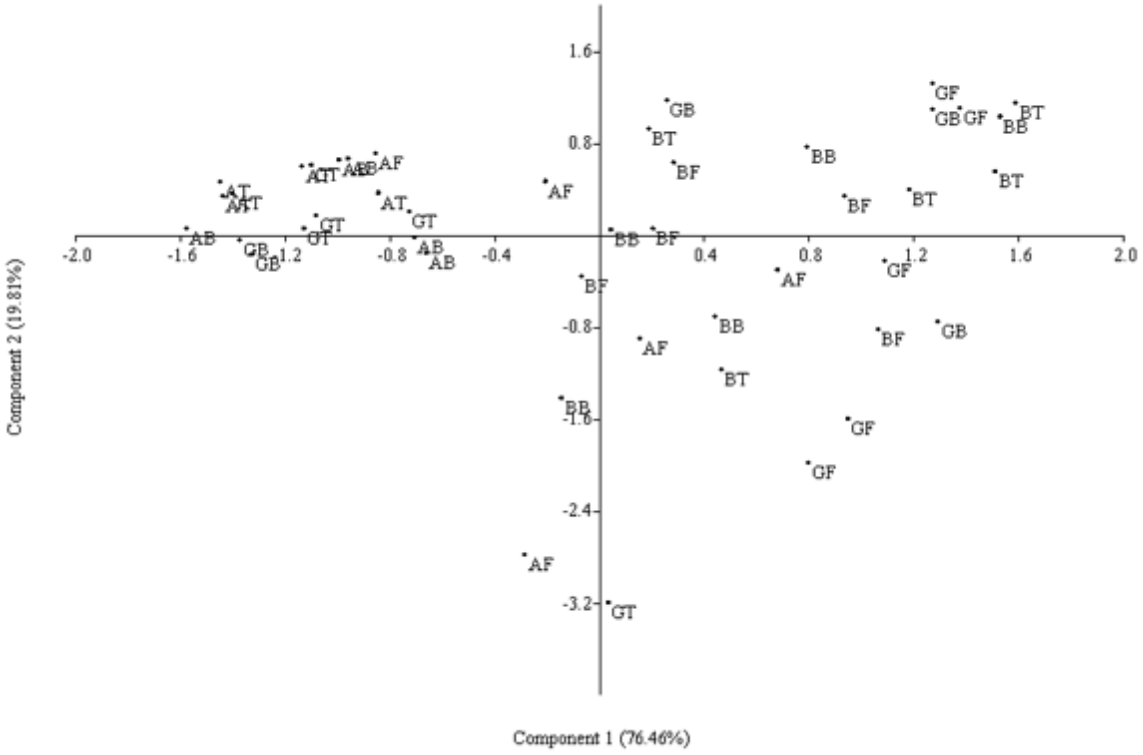

Figure 1-6: PCA of tree species density of mangroves in the estuaries at Antonina, Babitonga, and Guaratuba bays. Only the first two components are interpretable by the "Broken Stick" criterion. The percentage of each component is shown in the graphic. AF: Fringe Antonina bay plots; AB: Basin Antonina bay plots; AT: Transition Antonina bay plots; BF: Fringe Babitonga bay plots; BB: Basin Babitonga bay plots; BT: Transition Babitonga bay plots; GF: Fringe Guaratuba bay plots; GB: Basin Guaratuba bay plots; GT: Transition Guaratuba bay plots;

Discussion

As reported by other studies on Southern Brazil, three species (*A. schaueriana, R. mangle*, and *L. racemosa*) grow in the studied mangroves (Schaeffer-Novelli et al. 1990; Dornelles et al. 2006; Cunha et al. 2006b; Kilca et al. 2011; Martins et al. 2016). In fact, these species seems to have high tolerance to the environmental characteristics of subtropical regions, i.e. lower tidal amplitudes and temperatures, and coast lowland restricted by mountain ranges (Schaeffer-Novelli et al. 1990; Schaeffer-Novelli et al. 2000).

Mangroves closer to the equator develop under greater tidal amplitude, high solar radiation and temperatures, which favor the development of larger individuals (Schaeffer-Novelli et al. 1990).

The studied mangroves are lower than other found in Tropical regions but similar to those found in other mangroves from Southern and Southeastern of Brazil (Schaeffer-Novelli 1995; Sessegolo 1997; Carmo et al. 1998; Soares 1999; Carmo et al. 2000; Silva et al. 2005; Abreu et al. 2006; Matni et al. 2006). Previous studies have indicated that mangroves show low degrees of development, as for height and diameter, when exposed to temperature stressing conditions (Lovelock et al. 2007; Pellegrini et al. 2009). In higher latitudes, as in this study, air temperature may be a physiological barrier to the advance of mangroves (Soares et al. 2012) if dispersal barriers are inexistent.

The structure of southernmost Brazilian mangroves was characterized by the dominance of trees 10 m high with a strong gradient where trees reaches 2.5 m high in the innermost mangrove portion (Schaeffer-Novelli et al. 1990). In the three studied estuaries, larger individuals were found in fringe plots. A similar pattern of decrease in trees size between fringe and transitional mangroves has also been reported for other Brazilian mangroves (Pellegrini et al. 2000; Estrada et al. 2013). Studies suggest that, in transitional areas, smaller individuals may present morphological characteristics associated with nutritional limitations (Lin and Sternberg 1992; Lüttge 2007). This limitation is likely determined by gradients of tidal flooding frequency associated with topographic elevations (Estrada et al. 2013). In the studied mangroves, further specifics analyses evaluating nutrient usage by mangrove species in transition areas may help test the hypothesis that differences in structure are a response to local nutritional limitations.

Our results suggest that *A. schaueriana* develops in fringe forests and that its development and number of individuals decreases towards transition areas. The structure of fringe plots at Guaratuba Bay indicated that the occurrence of larger individuals of *A. schaueriana* might be associated with a greater contribution of silt particles in the substrate. In fact, *R. mangle* and *L. racemosa* are more associated with sandy substrates, while *A. schaueriana* often occurs in substrates containing finer particles, as silty-clay (Souza et al. 1993). However, this pattern occurs in mangroves with either low (as at Antonina and Babitonga Bays) or high pore water salinity (as at Guaratuba Bay). The decrease of *A. schaueriana* in transition plots may be linked to other factors (e.g. the arrival of propagules), in which water movement may limit their establishment due to low tide influence, as transitions plots. In fact, *A. schaueriana* preferentially occupies intertidal areas above sediments with high clay contents, along riverbanks or exposed to the shoreline (Schaeffer-Novelli 1999).

The greater contribution of *R. mangle* in the forest structure of Antonina Bay may be related to less disturbed environments. The species dominates upper estuarine areas in several mangroves of the Brazilian coast (Schaeffer-Novelli 1999) and previous studies suggest that *R. mangle* representativeness has been associated with less disturbed mangroves in southeastern Brazil. In mangrove forests highly subjected to disturbances, Rhizophoraceae species contribute less than species from other groups, as *Laguncularia* (Smith 1993; Soares 1999). Studies report the occurrence of *L. racemosa* in coastal, protected areas, and along canals washed by waters, with low salinity (Schaeffer-Novelli, 1999; Kilca et al., 2011), as we found in Babitonga Bay mangroves. In all plots of Babitonga Bay, *L. racemosa* showed higher density, dominance, CV and IV, supporting previous studies in the adjacent areas (Dornelles et al. 2006; Cunha et al. 2006b; Kilca et al. 2011).

At Guaratuba bay, *L. racemosa* and *R. mangle* are distributed in a zonation pattern, from fringe towards transition plots. Such zonation may be related to high tide influence, since the Pinheiros River estuary is located near the mouth of the bay. In these areas, mangroves are characterized as high-energy environments ruled by the dynamic of sandy fraction deposition (Sessegolo 1997). The influence of environmental conditions on the competitive ability of mangrove species probably reflects this distribution (Lima and Tognella 2012). The PCA with structural parameters shows that *L. racemosa* and *R. mangle* densities are mostly responsible for sorting sampling areas into groups that correspond to the analyzed bays. Since high density of *R. mangle* occurs with low *L. racemosa* density, it seems that the occurrence of both species is influenced by similar environmental parameters, but in opposite ways.

The studied mangrove forests showed distinct structures and compositions. As our results suggest, the differences in particle size of the substrate and salinity, due to the morphology of the estuary and distance from the coast, are crucial for species distribution in the mangrove forests of Antonina, Guaratuba, and Babitonga Bays. Differences in species distribution indicate that mangrove structure is strictly related to species plasticity and range of environmental tolerance. Each mangrove species showed a particular set of environmental requirements that resulted in distinct distribution patterns.

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CAPÍTULO 2

LINKING SUBTROPICAL BRAZILIAN MANGROVE FOREST STRUCTURE TO LOCAL ENVIRONMENTAL ATTRIBUTES AND SPECIES PREFERENCES

Submetido ao Brazilian Journal of Botany

Linking subtropical Brazilian mangrove forest structure to local environmental attributes and species preferences

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Abstract

Linking subtropical Brazilian mangrove forest structure to local environmental attributes and species preferences

This study characterizes the structure of three subtropical mangroves and correlates it to environmental conditions to verify (1) if tree species follow a distribution pattern in subtropical mangroves and (2) if it is modulated by sediment and nutrient composition. Fifteen 50 m^2 plots parallel to the river were demarcated in fringe (5), intermediary (5) and interior (5) mangrove areas along three subtropical estuaries of Southeastern Brazil: Antonina, Guaratuba, and Babitonga Bays. In each plot, we analyzed soil features, forest structure and tree species distribution. *Rhizophora mangle* L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, and *Laguncularia racemosa* (L.) Gaertn. occur in the studied mangrove forests. Each studied mangrove presented a pattern of species distribution. The mangrove structure were linked to differences in the distance from the coast, the physicochemical features along the floodplain gradient and the degree of tolerance that each species presents. Mangrove distribution and structure was strictly related to species tolerance to pore water salinity and to nutrient concentrations, as calcium and phosphorus. Our results indicated the significance of the distance from the coast, showing the weight of factors that vary in a local scale.

Keywords: *Avicennia schaueriana*, ecological zonation, *Laguncularia racemosa*, mangrove floodplain gradients, phytosociology, *Rhizophora mangle.*

Introduction

Mangroves represent a transition ecosystem between marine and terrestrial environments, which can be found under an extensive range of environmental settings (Kathiresan and Bingham 2001; Spalding et al. 2010). Variations in tides, salinity, winds, high temperatures, high irradiance and flooded sediments with low oxygen concentrations (Ball 2002; Hogarth and Hogarth 2007) require specific morphological and physiological strategies from mangrove tree species (Lovelock et al. 2006a; Sobrado and Ewe 2006b; Krauss et al. 2008). This set of strategies allows species to survive in the particular environmental conditions of mangroves (Lüttge 2008).

In mangroves, sediment features influence tree species distribution according to their ability to store and recharge water and nutrients (Adame et al. 2010; Bompy et al. 2014). The great variety of growing conditions is reflected in adaptable tree forms, spatial arrangements, and stand structural attributes (Lin and Sternberg 1992; Sobrado and Ewe 2006b; Urrego et al. 2014). The definition of structure and distribution patterns of species in mangroves has been reported since the first studies (Pool et al. 1977; Cintron and Novelli 1984; Smith 1992), in an attempt to clarify the processes and dynamic variables influencing its configurations (Lugo and Snedaker 1974; Schaeffer-Novelli et al. 1990). Despite low species diversity, several patterns of structure and species distribution related to environmental conditions have been found (Lacerda 2009; Spalding et al. 2010).

Mangrove forests occur along the Brazilian coast from northernmost (State of Amapa) to southern regions (State of Santa Catarina) (Schaeffer-Novelli et al., 2000). In southern Brazilian mangroves, a subtropical ecosystem, three woody species are found: *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia schaueriana* Stapf & Leechm. ex Moldenke (Acanthaceae), and *Laguncularia racemosa* (L.) Gaertn. (Combretaceae). Subtropical mangroves are still poorly comprehended and Brazilian subtropical mangrove areas are not exception. Despite some studies that shows local structural patterns (Lin and Sternberg 1992; Suwa et al. 2009; Soares et al. 2012), in subtropical mangroves, there is still a lack of knowledge about structure and the ecophysiological processes linked to species distribution and development (Medina 1999; Lacerda 2009; Soares et al. 2015).

Previous studies have shown different patterns of structure revealing the ecosystem complexity even when mangroves are geographically close (Bigarella 2001; Matni et al. 2006; Abreu et al. 2006b; Kilca et al. 2011; Urrego et al. 2014; Calegario et al. 2015). Many studies support the influence of abiotic variables on the structure and distribution of mangrove tree species (Snedaker 1982; Lovelock et al. 2006a; Sobrado and Ewe 2006b; Krauss et al. 2008; Sinfuego and Buot 2013), which may lead to different structure among mangrove forests. The set of environmental factors that represents changes in distance from

cost and also from the main water body, e.g. fluctuations in salinity and water availability, was previous associated to reduction of structure development in mangroves (Lugo et al. 2007). Also, the distance from the coast influence inputs of nutrients and organic matter from uplands and intertidal wetlands (Cifuentes et al. 1996; Krauss et al. 2008), which may be associated to sclerophylly and alteration in mangrove architecture (Parida and Jha 2010).

Thus, in order to evaluate the influence of environmental parameters on the distribution of tree species in mangroves of three subtropical bays, this study aims to address the following hypothesis: (1) the distance from the coast modulate mangrove forest structure, through changes in salinity and other dependent variables, such as pH e nutrient concentration; (2) the floodplain gradient also represents a gradient of salinity, organic matter content and sediment grain size that respond to local variations, this gradient limits species distribution inside each mangrove; We expect to find different mangrove forests structure linked to different distances from the coast, with a strong correlation among mangrove forest structure and soil parameters as salinity, organic matter content and nutrient concentrations. Also, if the second hypothesis is true, the result is a different zonation pattern within each mangrove correlated to environmental variables that are modulated by the floodplain gradient.

Methods

Study Area - This study was conducted in three estuaries in southern Brazil: Antonina Bay, Guaratuba Bay and Babitonga Bay (Fig. 1). Climate conditions are similar among estuaries, classified as mesothermal (*Cfa*) in the Köppen System.

Despite the bays being on similar latitudes, particular geographic differences among the studied estuaries should be highlighted: the Estuary of Nhundiaquara River is located in the inner portion of the Antonina Bay (Brazil, between 25º29'S - 25º28'S and 48º41'W - 48º44'W). The Antonina Bay consists in the innermost bay along the current Brazilian coastline (Lana et al. 2001), about 35 kilometers away from the coastline. The average temperature is 20.5° C, with 16.7° C and 26.4° C minimum and maximum values, respectively. The annual precipitation is 2 773 mm (Meteorological System of State of Parana/SIMPEPAR). This bay is under a semi-diurnal tides regime ruled by the reflux tides, classified as microtidal. In general, Antonina Bay soils are characterize by poorly to very poorly select sediments (Lana et al. 2001).

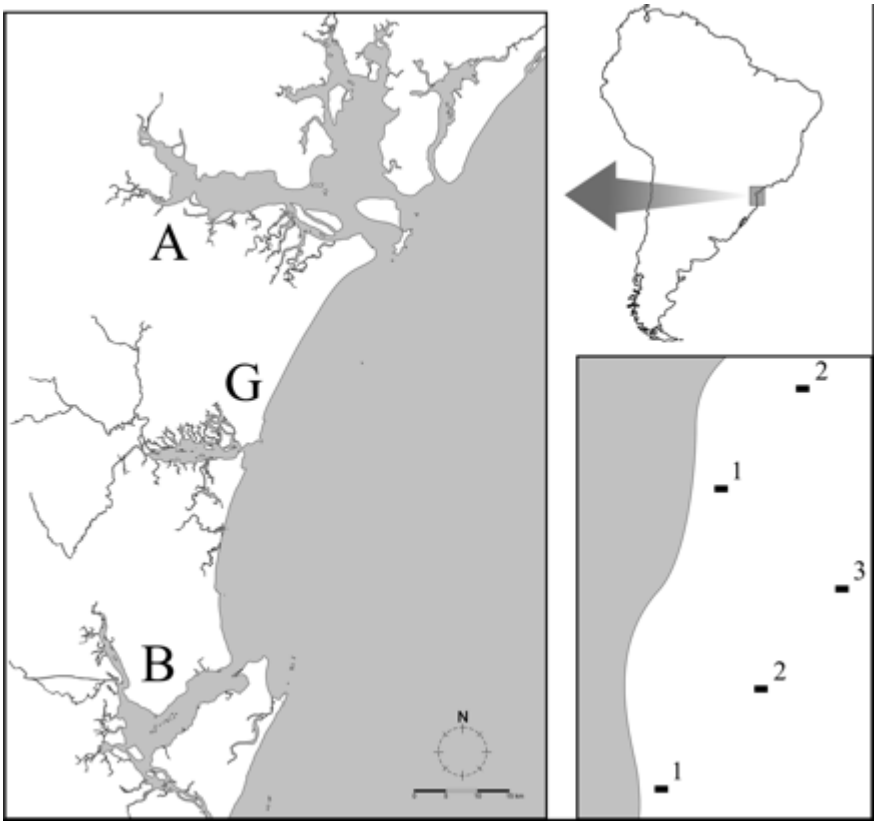

Figure 2-1: Map of Brazil, showing the location of the studied mangroves in the subtropical coastline: Antonina Bay (A), Guaratuba Bay (G) and Babitonga Bay (B). Plots were allocated at different distances from the water body, based on field observations, in order to represent the floodplain gradient: fringe plots (1), intermediary plots (2) and interior plots (3).

The Estuary of Pinheiros River is located close to the mouth of the Guaratuba Bay (Brazil, between 25º50'S - 25º48'S and 48º34'W - 48º36'W), around 4 kilometers distant from the coastline. The average annual rainfall is around 3183 mm and the average temperature is 14.5° C in the winter season and 29.6° C in the summer (Meteorological System of State of Parana/SIMPEPAR). This bay is also classified as microtidal, ruled by semi-diurnal tides regime, with changes in average amplitude due to possible occurrence of storm floods associated with high winds (Marone et al. 2005). There is a pronounced saline stratification, intensified in neap tide and low discharge of fresh water in the system (Marone et al. 2005). The morphology of the estuary is characterized by sandy sediments, due to the intensity of the currents that prevents the deposition of fine sediment and transports part of the most fine sand to adjacent areas (Cotovicz Junior et al. 2014).

The Estuary of Palmital River is located in the middle portion of the Babitonga Bay (Brazil, between 26º12'S - 26º06'S and 48º45'W - 48º47'W), around 20 kilometers away from the coastline. The average temperature is 16.5º C in the winter season and 25.9º C in the summer (Bartz et al. 2015). The annual rainfall is around 2265 mm (Agricultural

Research and Rural Extension of the State of Santa Catarina/EPAGRI). The Babitonga Bay is characterized as microtidal and is ruled by a semi-diurnal tides regime (Vieira et al. 2008). The Estuary of Palmital River is under dominance of the flood tide with amplification tide height in the innermost areas, due to the effects of the narrowing of the main channel (Vieira et al. 2008). The morphology of the sediment has greater homogeneity in the Estuary of Palmital River, ranging from sand to mud.

Fifteen 50 m^2 plots were established, parallel to the river along each estuary, to characterize mangrove structures, totaling 45 plots. The size of the plots was fixed based on previous studies (Madi et al, no prelo), which indicated that 50 m^2 plots were able to characterize subtropical Brazilian mangrove forests. We allocate plots using a random method. Considering that the mangrove is not continuous and fixed-width, plots were allocated at different distances from the water body based on field observations in order to represent the floodplain gradient. Also, plots were established at different distances among each other, to avoid local topographic variations. They were classified into zones inside the floodplain gradient, simplifying the classification of Schaeffer-Novelli et al. (2000): five fringe plots, representing the section close to the river; five intermediary; and five interior plots, representing the section of transition between mangrove and Lowland Rainforests (Fig 1).

Abiotic factors - Salinity of pore water was measured at 30 cm depth at low tide with a digital hydrometer (Akso AK83) in five randomly selected points within each plot. Seventy-five samples were obtained per bay. Two samples of sediment from each plot were collected at low tide. Particle size distribution (30 cm depth) was determined using a particle analyzer (Raij et al. 2001). To determine sediment nutrient composition, samples were collected at two depths (0 to 10 cm and 10 to 30 cm depth) and analyzed according to Raij et al. (2001). Procedures followed standard methodology to organic matter content, pH values, nutrient composition of sediment (fractions of total P, K, Mg, Ca, Na, Fe, Mn, Zn and Cu) and cation exchange capacity for the <2 mm fraction, as described in Camargo et al. (2009).

Vegetation Structure - In each plot, all of the living individuals were identified at the species level. We measured the diameter at breast height (DBH, cm), according to Mueller-Dombois and Ellenberg (1974). Height (m) was recorded for all individuals at least one meter high, in addition to describing the condition of each trunk (alive or dead). Height was estimated with a hypsometer and DBH with a diameter tape. For *R. mangle*, trunk diameter was always measured above the highest stilt root. When individuals presented multiple stems, the area of each stem was calculated. All stems areas were added and the diameter of the representative area of all steams were calculated. The total diameter was considered DBH

to these individuals. Density of species and dead trunks in each plot were calculated according to Mueller-Dombois and Ellenberg (1974). Dead trunks phytosociological parameters were calculated separately from living individuals.

Data analysis - Means (± standard deviation) were calculated for all quantitative variables. Analyses were performed using the software "R" (R Development Core Team, 2009) with the "vegan" and "labdsv" packages (Roberts and Roberts 2007). Values were considered significant at $p \leq 0.05$. In all cases, we tested the homogeneity of the variances and, when necessary, data was log-transformed. We performed a two-way Analysis of Similarity (ANOSIM, plots nested in areas) to show similarities among soil parameters of bays. A Two-way Analysis of Variance (ANOVA) was used to compare soil parameters among bays and among sections inside each mangrove. Post-hoc Tukey's test was performed to test for differences between pairs of means.

To visualize differences among areas and among plots in each area, we performed a Principal Component Analysis (PCA) based on the covariance of sediment variables (pore water salinity, organic matter content, pH, and particle size distribution – clay, silt, and sand content). To visualize the distribution of tree community, we used a Non-metric Multidimensional Scaling (NMDS) analysis performed using the density of each species and the density of dead in each section inside mangroves as parameters, based on Bray-Curtis distances. We used a two-way ANOVA to elucidate how structural development and species distribution varies according to the distance from the coast and plots inside each mangrove. We performed a post-hoc Tukey's test to test for differences between pairs of means.

Model of multivariate analysis of variance was constructed using Distance Based Redundancy Analysis (dbRDA) using Gower distances with the function “capscale” of the “vegan” package (Oksanen et al. 2007) to determine the most influential environmental variables (areas, plots and soil parameters: pore water salinity, clay, silt and sand content, organic matter content, pH, macro and micronutrients soil content) on the tree community composition (Legendre and Andersson 1999). Soil parameters were standardized by standard deviation. We tested the significance of each predictor with 999 permutations through ANOVA.

Results

Abiotic factors - Particle size distribution analysis showed differences among areas. Fringe sediments in Antonina presented silty-clay texture, while intermediary and interior plots presented clay-loam texture. In Babitonga, fringe sediments are classified as clay-loam

texture, while intermediary and interior sediments are classified as clay and sandy-clay-loam. Guaratuba sediments presented higher content of sand, although sediment of all plots was classified as loam (Table 1). There were no variations in pore water salinity within estuaries (two-way ANOVA F: 0.52, $p>0.05$, n=45), but values differed among estuaries: Guaratuba presents higher pore water salinity, followed by Antonina and Babitonga Bays (ANOVA, F: 210.6, $p<0.0001$, n=225) (Table 1).

The two-way ANOSIM showed differences in nutrient concentrations among bays (global R=0.39, $p<0.0001$) and among sections inside each mangrove (R=0.14, $p<0.01$). Sediments at the Antonina Bay have higher organic matter (ANOVA, F: 9.71, $p <0.001$) and silt contents (ANOVA, F: 11.11, $p<0.0001$), whereas, at the Guaratuba Bay, sediments showed higher pH values (ANOVA, F: 3.11, $p=0.02$). There were no differences among the sediments of fringe, intermediary and interior plots at the Guaratuba Bay. At the Antonina Bay, fringe plots had higher pH (ANOVA, F: 4.6, $p=0.02$) and phosphorus content (ANOVA, F: 8.8, $p<0.001$). At the Babitonga Bay, phosphorus content was higher in intermediary plots (ANOVA, F: 4.0, $p<0.001$). Details of all nutrient concentration for the three studied bays are available in tables S1 to S3 in the supplementary material (Anexo).

Table 2-1: Mean values (± standard deviation) of pore water salinity (‰), pH, organic matter content (OM, 10 cm deep, $g.dm^{-3}$), Phosphorus content (P, 10 cm deep, $mmol_c.dm^{-3}$), Calcium content (Ca, 10 cm deep, $mmol_c.dm^{-3}$) and particle size content (clay, silt, and sand, %) from sediments at the Antonina Bay, Guaratuba Bay, and Babitonga Bay (Brazil).

Plots	Pore water salinity	pH	OM	P	Ca	Clay	Silt	Sand
	Antonina Bay							
Fringe	16.8 ±3.8a	4.8 ±0.4a	75.8 ±11.8a	30.2 ±15.7a	55.5 ±13.2a	41.2 ±11a	47.2 ±13a	11.6 ±23a
Intermediary	15.9 ±3.7a	4.1 ±0.3b	89.8 ± 6.0a	12.6 ±6.6b	51.6 ±13.3a	31.2 ±6b	45.0 ±17a	23.8 ±23a
Interior	18 ±3.2a	4.1 ±0.2b	89.0 ± 5.4a	9.0 ±1b	49.0 ±4.5a	27.5 ±7b	51.6 ±17a	20.9 ±24a
	F=0.31;	F=6.50;	F=0.15;	F=4.68;	F=2.97;	F=14.04;	F=0.31;	F=2.35;
	P>0.05	P<0.05	P<0.05	P<0.05	P>0.05	P<0.05	P>0.05	P>0.05
	Guaratuba Bay							
Fringe	22.4 ±2.8a	4.8 ±0.8a	73.8 ± 8.7a	12.8 ±2.7a	53.6 ±16.8a	26.1 ±14a	36.7 ±11a	37.2 ±24a
Intermediary	19.8 ±3.4a	4.9 ±0.4a	58.5 ±19.1a	9.5 ±3.9a	39.5 ±10.6a	22.2 ±11a	33.0 ±7a	44.8 ±14a
Interior	20.9 ±4.4a	4.9 ±0.3a	71.5 ±16.1a	13.5 ±6.7a	48.3 ±15.1a	26.3 ±21a	29.7 ±17a	44.0 ±13a
	F=0.63;	F=0.25;	F=0.61;	F=0.92;	F=0.15;	F=0.10;	F=0.39;	F=0.27;
	p>0.05	P<0.05	P>0.05	P>0.05	P>0.05	P>0.05	P>0.05	P>0.05
	Babitonga Bay							
Fringe	9.6 ±4.6a	4.6 ±0.4a	75.2 ±18.5a	16.8 ±6.9a	50.3 ±14.8a	37.0 ±15a	32.4 ±16a	30.6 ±7b
Intermediary	8 ±4.8a	4.7 ±0.4a	87.2 ±10.2a	18.2 ±3.6a	57.2 ±8.8a	52.0 ±21a	17.5 ±3b	30.5 ±22b
Interior	6.8 ±3.9a	4.2 ±0.8b	85.8 ±12.8a	9.3 ±3.2b	61.0 ±15.9a	27.1 ±27a	12.7 ±6b	60.2 ±21a
	F=0.46;	F=4.31;	F=1.68;	F=0.77;	F=4.02;	F=1.69;	F=4.44;	F=4.33;
	p>0.05	P<0.05	P>0.05	P>0.05	P=0.05	P>0.05	P<0.05	P<0.05

PCA showed that bays overlap in distribution (Fig. 2). Soil texture attributes summarized most of data variance (60%). The first axis (PCA1) explained 36% of data variance and was mainly represented by sand content (eigenvector 0.56) and organic matter content (eigenvector -0.47). The second axis (PCA2) summarized 24% of data variance, mainly represented by pore water salinity (eigenvector 0.67) and silt content (eigenvector 0.52).

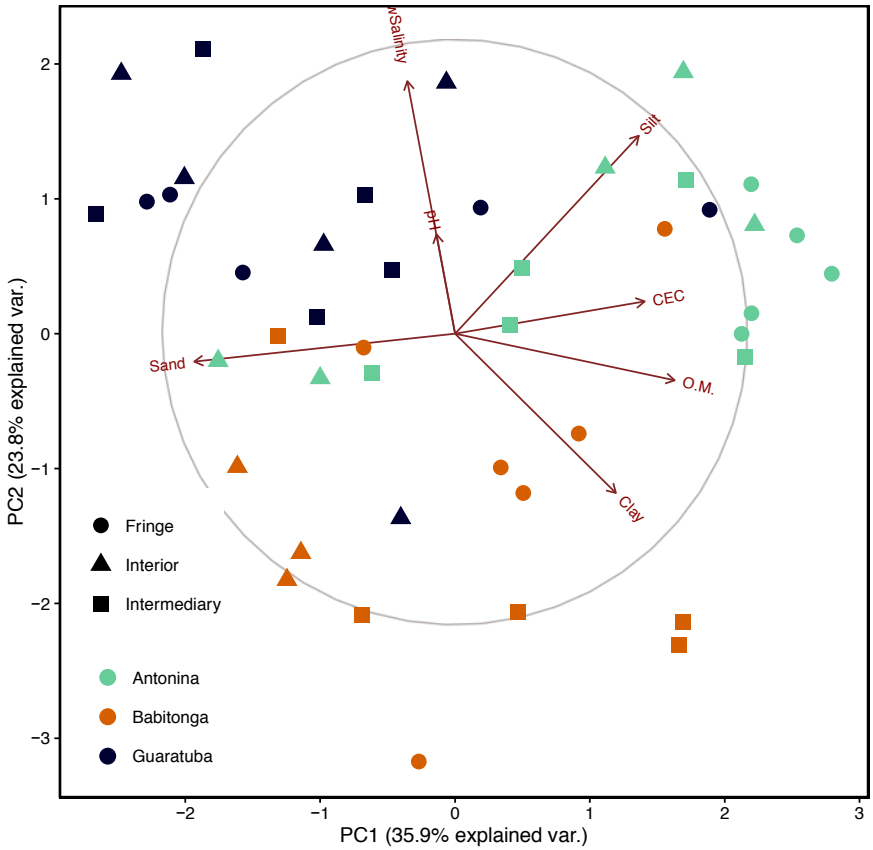

Figure 2-1: Principal Component Analysis with soil attributes: sand, silt and clay content, pore water salinity (PWSalinity), organic matter content (O.M.), pH and cation exchange capacity (CEC). The first axis (PCA1) explained 36% of data variance and was mainly represented by sand content (eigenvector 0.56) and organic matter content (eigenvector -0.47). The second axis (PCA2) summarized 24% of data variance, mainly represented by porewater salinity (eigenvector 0.67) and silt content (eigenvector 0.52). Only the first two axes were interpreted according to the “Broken stick” criteria.

Vegetation structure - *A. schaueriana, R. mangle*, and *L. racemosa* occurred in all studied mangroves. These species showed a wide variation in density among bays and along the floodplain gradient. Dead trunks were found in all areas. They were

more numerous at the Antonina Bay and presented higher DHB in the Babitonga Bay.

At the Antonina Bay, we counted 277 individuals, among which 16 *A. schaueriana*, 49 *L. racemosa*, and 197 *R. mangle*, in addition to 15 dead trunks. In Guaratuba Bay, we surveyed 209 individuals, including 21 *A. schaueriana*, 84 *L. racemosa*, 90 *R. mangle*, and 13 dead trunks. At the Babitonga Bay, we counted 154 individuals: including 25 *A. schaueriana*, 88 *L. racemosa*, and 34 *R. mangle*, and 7 dead trunks. The NMDS indicated that the community was significantly related to both gradients: the section inside each mangrove that represents the floodplain gradient and the distance from the coast that varies among bays that represents mainly a gradient of pore water salinity (Stress = 0.13). Despite such relationship, plots ordination showed overlapping (Fig. 3).

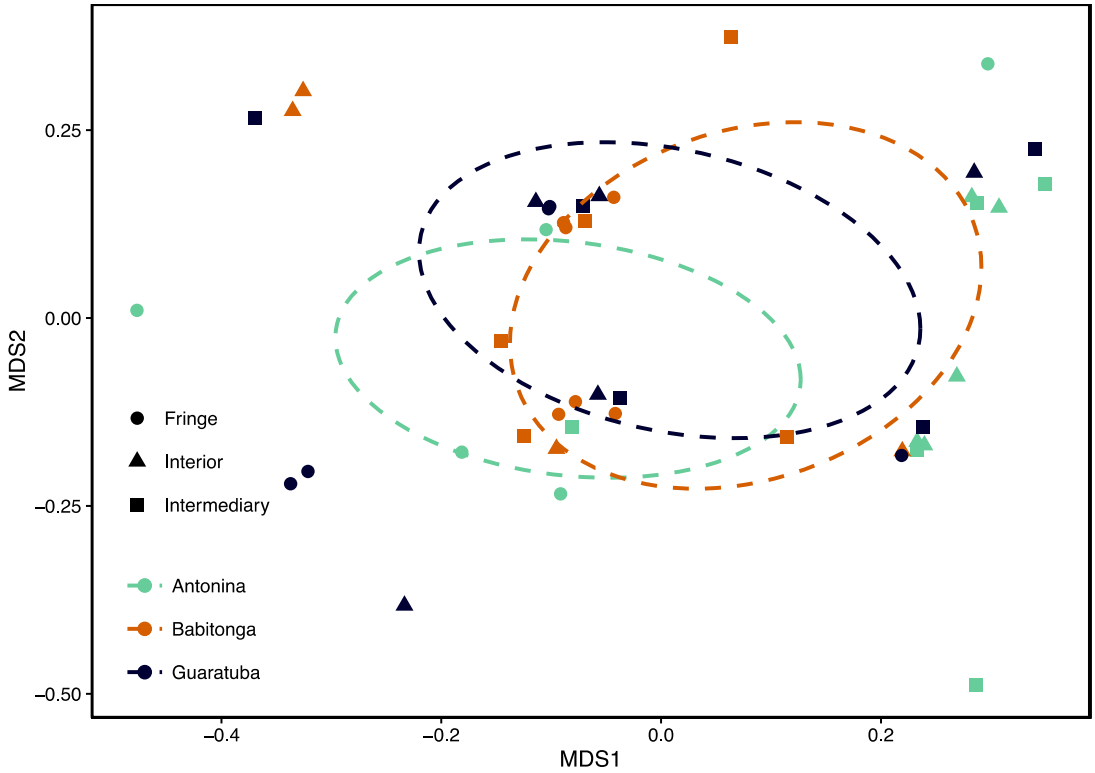

Figure 2-3: Non-metric Multi-Dimensional Scaling (NMDS) ordination diagram of plots showing variations in forest structure of mangrove forests in the Antonina Bay, Guaratuba Bay, and Babitonga Bay (Brazil). Stress value for the NMDS ordination is 0.13.

At the Antonina Bay, species showed differences among areas along the floodplain gradient (Table 2). *R. mangle* had the highest in all plots. *A. schaueriana* showed more developed individuals in fringe plots (Table 2), with individuals showing DBH larger than 30 cm.

At the Guaratuba Bay, *A. schaueriana* showed higher individuals and larger average DBH (Table 3). Species distribution presented a zonation pattern. In fringe plots, *L. racemosa* showed higher density. In intermediary plots, *L. racemosa* and *R. mangle* exhibited similar structure and distribution. In interior plots, *R. mangle* had higher density.

At Babitonga Bay, *L. racemosa* also presented a larger DBH in all studied plots. We found no differences among plots in the Babitonga Bay regarding structural parameters: *L. racemosa* exhibited higher density in all plots (Table 4).

Table 2-3: Mangrove vegetation structure in the Nhundiaquara River estuary, Antonina Bay, Paraná, Brazil. Values are shown by floodplain gradient (fringe, intermediary and interior plots) and species (*Avicennia schaueriana*, *Laguncularia racemosa*, and *Rhizophora mangle*). Heights mean values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation).

	General mean	*A. schaueriana*	*L. racemo*sa	*R. mangle*	Dead Trunks
Height (m)					
Fringe	8.5±0.4	9.6±5.9	5.3±3.0	6.5±3.7	2.0±2.7
Intermediary	7.5±1.0	1.1±2.4	5.4±3.3	7.8±1.2	4.2±3.9
Interior	6.5±1.1	-	6.2±1.5	6.6±1.4	2.9±2.6
DBH (cm)					
Fringe	15.4±4.2	69.5±62.8	32.4±15.1	46.4±26.3	26.3±7.5
Intermediary	9.1±1.5	11.14	9.6±3.6	8.6±3.4	8.9±1.5
Interior	8.5±2.0	-	9.0±2.9	7.3±1.9	10.7±1.4
Density (trunks.ha^{-1})					
Fringe	2800±1058	600±648	840±589	1280±355	120±178
Intermediary	3640±1053	40±89	560±384	2840±640	320±303
Interior	4650±1011	-	560±167	3800±525	160±167

Table 2-4: Mangrove vegetation structure in the Pinheiros River estuary, Guaratuba Bay, Paraná, Brazil. Values are shown by floodplain gradient (fringe, intermediary and interior plots) and species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*). Height means values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation).

	General mean	*A. schaueriana*	*L. racemo*sa	*R. mangle*	Dead Trunks
Height (m)					
Fringe	5.4±1.3	7.6±4.9	4.3±0.5	3.0±2.7	3.2±3.0
Intermediary	4.2±0.7	2.9±2.7	4.4±0.9	3.8±2.6	1.5±2.1
Interior	4.3±1.1	4.7±3.1	2.7±1.6	4.0±0.5	4.2±2.9
DBH (cm)					
Fringe	16.9±5.3	22.6±15.5	12.8±7.4	9.3±8.8	6.5±6.1
Intermediary	9.2±1.3	7.2±6.6	8.2±0.9	6.8±4.1	2.4±2.3
Interior	12.1±3.8	14.9±11.8	11.8±7.5	8.5±2.4	2.5±2.4
Density (trunks.ha^{-1})					
Fringe	1920±807	400±316	1360±864	120±109	200±244
Intermediary	3240±1080	200±240	1400±593	1480±1331	160±260
Interior	3040±1346	240±216	600±260	2040±1306	160±260

Table 2-5: Mangrove vegetation structure in the Palmital River estuary, Babitonga Bay, Santa Catarina, Brazil. Values are shown by floodplain zone (fringe, intermediary and interior plots) and species (*Avicennia schaueriana*, *Laguncularia racemosa* and *Rhizophora mangle*). Height means values (m, ± standard deviation), DBH: diameter at breast height mean values (cm, ± standard deviation).

	General mean	*A. schaueriana*	*L. racemo*sa	*R. mangle*	Dead Trunks
Height (m)					
Fringe	7.2±0.8	7.3±1.8	7.9±0.4	6.1±0.3	2.8±1.3
Intermediary	5.9±0.7	6.3±2.8	6.3±1.0	4.2±1.1	1.6±1.0
Interior	4.8±1.0	4.1±2.7	4.6±1.7	1.9±1.0	2.5±1.4
DBH (cm)					
Fringe	17.5±5.6	18.1±8.4	22.3±9.95	7.9±1.2	4.03±4.0
Intermediary	14.9±3.3	7.3±8.0	14.9±2.6	16.1±6.3	6.48±6.1
Interior	20.2±8.0	11.8±11.4	20.9±10.1	5.5±6.6	8.11±10.2
Density (trunks.ha^{-1})					
Fringe	2400±557	400±309	1200±379	560±408	100±167
Intermediary	1960±767	360±167	1120±912	400±244	80±108
Interior	1900±871	200±163	1250±700	350±574	100±115

The two-way ANOVA showed that species development and distribution respond differently to the distance form the coast and to plots inside each mangrove. *A. schaueriana* showed DBH (ANOVA, F: 6.3, p=0.004), height (ANOVA, F: 11.5, p<0.001) and density (ANOVA, F: 4.9, p=0.01) higher in fringe plots, although the distance from the coast seems not to affect those parameters (ANOVA, p>0.05). *L. racemosa* development and distribution seems to be more affected by the distance from the coast than by plots. The height (ANOVA, F: 9.2, p<0.0001) and DBH (ANOVA, F: 13.9, p<0.0001) of *L. racemosa* were lower in Guaratuba Bay than in both Antonina and Babitonga mangroves.

On the other hand, *R. mangle* structure and development respond to distance from the coast, to plot location and to its interaction effects, as well. The density of *R. mangle* was lower in Babitonga Bay (ANOVA, F: 20.6 p < 0.0001), however, its also respond to plot locations (ANOVA, F: 10.06, p <0.001), showing higher density in interior plots both in Antonina and Guaratuba mangroves. While the height of *R. mangle* was lower in Guaratuba, related to the distance from the coast (ANOVA, F: 10.23, p<0.001), the DBH was higher in fringe plots in Antonina and Guaratuba and higher in intermediary plots in Babitonga mangroves, affected by the interaction of the distance from the coast and plots location (ANOVA, F: 3.92, p = 0.03). Dead trunks distribution and structure were not affected neither by distance from the coast nor by plots inside each mangrove.

Structure x abiotic factors analysis - The dbRDA based model selection indicated that environmental drivers shaped the diversity and composition of mangrove tree species in the studied mangroves (ANOVA, F=1.41, p=0.01, Fig. 4). The first two constrained principal coordinates (dbRDA) were significant to explain 60% of forest structure variance. dbRDA 1 explained 31% of forest structure variance related to the number of *R. mangle* individuals (score -0.72) and DBH of *A. schaueriana* (score 0.84), while dbRDA 2 explained 29% of forest structure variance related DBH of *L. racemosa* (score -0.73) and *A. schaueriana* (score 0.56). Post-hoc tests also showed that the distance from the coast is the main driver (ANOVA, F=3.91, p<0.0001), followed by the different plots inside each mangrove (ANOVA, F=1.78, p=0.04), calcium (ANOVA, F=2.24, p=0.02) and phosphorus contents (ANOVA, F=1.90, p=0.05) as the most significant factors affecting mangroves forest structure.

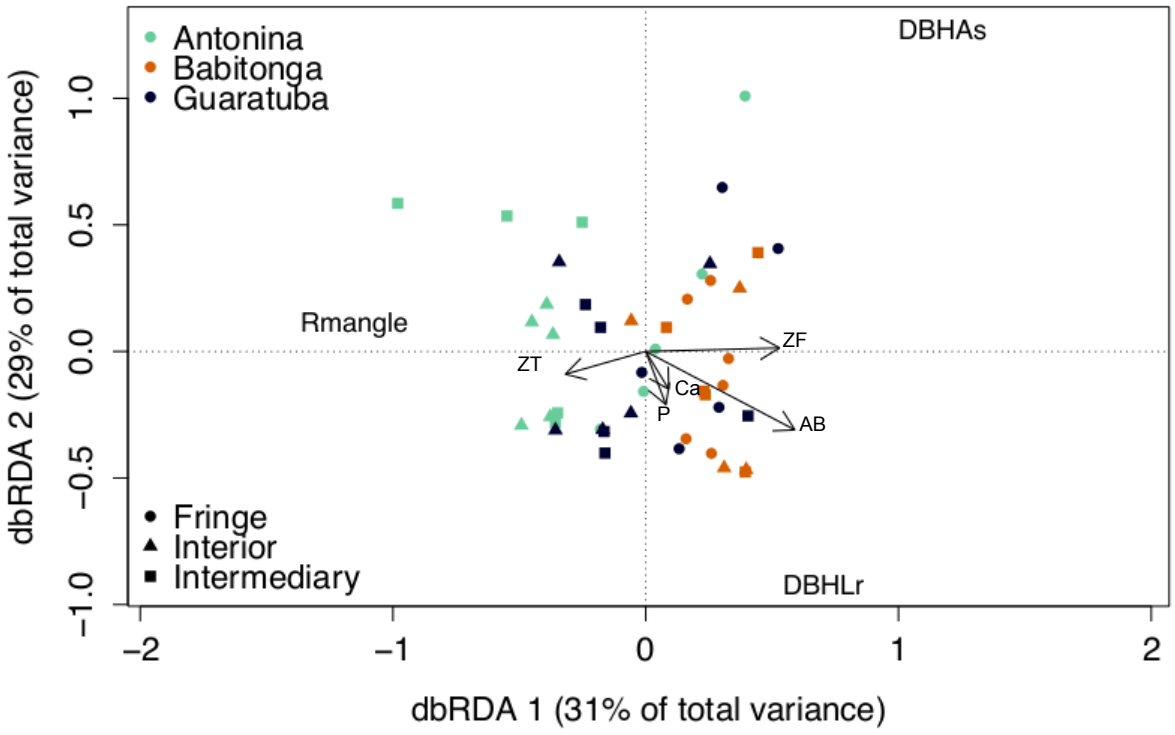

Figure 2-4: Distance-based Redundancy Analysis (dbRDA) showing the constrained ordination of samples relative to the explanatory variables. Sites were qualitatively grouped according to the first two constrained principal coordinates (dbRDA), which were significant to explain 60% of forest structure variance of mangroves of the Antonina Bay, Guaratuba Bay, and Babitonga Bay (Brazil). dbRDA 1 explained 31% of forest structure variance related to the number of *R. mangle* individuals (Rmangle, score -0.72) and DBH of *A. schaueriana* (DBHAs, score 0.84), while dbRDA 2 explained 29% of forest structure variance related DBH of *L. racemosa* (DBHLr, score -0.73) and *A. schaueriana* (score 0.56). Bays (BA – Antonina Bay, BB- Babitonga Bay, BG – Guaratuba Bay), zonation (ZF – Fringe zone, ZB – Intermediary zone, ZT – Interior zone), calcium (Ca) and phosphorus contents (P) were the main factors affecting mangroves forest structure.

Discussion

As reported by other studies in Southern Brazil (Schaeffer-Novelli et al. 1990; Dornelles et al. 2006; Cunha et al. 2006b; Kilca et al. 2011), all three species (*A. schaueriana, R. mangle*, and *L. racemosa*) grew in the studied mangroves but with differences in structure and distribution. Each studied mangrove presented a pattern of species distribution linked to differences in physicochemical factors along the floodplain gradient and the degree of tolerance that each species presents.

The PCA performed with soil characteristics showed that sand and organic matters contents were the most important attributes grouping areas into their respective bays, despite small overlapping. Indeed, species showed some distribution pattern related to particle size distribution in Guaratuba Bay: *R. mangle* and *L. racemosa* distribution can be related to sandy substrates, while *A. schaueriana* is more associated with substrates containing finer particles, such as silty-clay. But the Antonina and Babitonga areas did not show species distribution patterns related to particle size content. Although there is a correlation between species distribution and soil particle size, it is known that this distribution pattern does not occur in all mangroves (Schaeffer-Novelli et al. 2000; Silva et al. 2005; Dornelles et al. 2006; Cunha et al. 2006b) and several combinations of species distribution and particle size of sediment composition can happen (Camargo Maia and Coutinho 2012; Calegario et al. 2015).

In the three studied estuaries, larger individuals were found in fringe mangroves. A similar pattern of decrease in tree size between fringe and interior areas has also been reported for other Brazilian mangroves (Pellegrini et al. 2009; Estrada et al. 2013). Indeed, the structure of southernmost Brazilian mangroves was characterized by the occurrence of 10 m high trees, with a strong gradient in which the innermost mangrove portion trees reached 2.5 m (Schaeffer-Novelli et al. 1990). Studies suggest that, in interior areas, smaller individuals may present morphological characteristics associated with nutritional limitations (Lin and Sternberg 1992; Lüttge 2007). Our results showed that Antonina fringe plots exhibited higher pH and phosphorus contents, which can explain the higher structural development of mangrove species. Unlike mangroves in the Antonina Bay, there is no structural difference among plots at Babitonga Bay mangroves.

Mangroves in the Guaratuba Bay exhibited a zonation pattern of species distributions although the sediments measured variables were not significantly different. It seems that the higher pore water salinity may accentuate alterations in soil nutrients content and species requirements. Several studies have indicated the following trend of salt tolerance in mangrove species: *Avicennia* > *Laguncularia* > *Rhizophora* (Tomlinson 1986; Medina 1999;

Sobrado and Ewe 2006b). Since the degree of salinity among soil particles may inhibits uptake and reduction of nutrients, the higher pore water salinity results in ionic instability (Kao et al. 2004; Parida and Jha 2010). Thus, the degree of salinity tolerance may also be related to nutrient sensitivity in mangrove species (Lüttge 2008).

In Guaratuba Bay, *R. mangle* seems to have greater competitive ability in interior plots, which may indicate a different range of salinity tolerance, related to a low frequency of tidal inundation. However, both *A. schaueriana* and *L. racemosa* distribution decreases from fringe towards interior areas. To *A. schaueriana,* the decrease towards interior areas occur also in both Babitonga and Antonina Bay, but *L. racemosa* does not express same pattern in the other studied bays. This result may indicate that, in Guaratuba Bay, the proximity to the coastline may impact other environmental conditions not addressed here. Further studies about the ecophysiological strategies to tolerate the local dynamic of salinity may elucidate the acting processes that result in the zonation pattern expressed.

Both the Antonina and Babitonga Bays exhibit low pore water salinity. It may be also related to the distance from the coast, which is more similar between Antonina and Babitonga, than those and Guaratuba. It appears that the fresh water of mountain rivers around the bays flows into the estuary and keeps salinity low. Antonina and Babitonga mangroves showed higher individuals than Guaratuba mangroves, which may indicate a better development of mangroves in lower salinity conditions. However, though Antonina and Babitonga plots present low pore water salinity when compared to Guaratuba Bay mangroves, the dbRDA showed greater distinction between Antonina and Babitonga forest structure, associated with the occurrence of *R. mangle* and *L. racemosa*.

Despite being described as similar in salt tolerance (Parida and Jha 2010), the occurrence of *R. mangle* and *L. racemosa* indicated that species differ in requirements and preferences. In the studied mangroves, *R. mangle* occurrence, DBH of *L. racemosa* and DBH of *A. schaueriana* represent the main variation among plots and are linked to calcium and phosphorus soil content. These structural attributes characterize how species respond to different nutrient niches. Other studies also found subtropical mangroves where *R. mangle* and *L. racemosa* structural features seem to represent the limits of a nutrient tolerance gradient (Sessegolo 1997; Bigarella 2001; Dornelles et al. 2006; Kilca et al. 2011). Urrego et al. (2014) suggest that *R. mangle* can be found in areas with high calcium and magnesium concentrations, due to its higher efficiency in rejecting Na from the root environment and thus higher selectivity to nutrients, while *L. racemosa* seems to be insensible to calcium variations in mangrove soils, occurring in soils with both low and high calcium concentration. *Avicennia* spp. were positively related to pH, since it seems to be more efficient in water usage and, therefore, to have a higher salt tolerance (Lovelock 2004).

In the studied mangroves, we found low values of pH, which may impacts phosphorus availability and calcium content (Ukpong 2000; Krauss et al. 2008; Lima and Tognella 2012). In pH lower than 4.5, as found in the mangroves studied here, soil calcium concentration may maintain the permeability of cell membranes. The effect known as the Viets effect (Viets 1944) proposes that, in low pH soils, the absorption of other nutrients by plants is modulated by soil calcium concentration. Previous studies suggest these soil components as crucial to forest development and specially to support the occurrence of species with distinct tolerance to nutrients limitations (Ukpong 2000; Mendoza et al. 2012; Urrego et al. 2014).

Phosphorus is widely known as a limiting factor to mangrove species occurrence and distribution since phosphorus is required to several physiological processes, e.g. store and transfer of energy and photosynthesis (Krauss et al. 2008) and it cannot be replaced by biological fixation (Lovelock et al. 2007). Previous studies indicate several mangrove forests are limited by the availability of P (Lin and Sternberg 1992; Feller et al. 2003; Lovelock 2004; Lovelock et al. 2007).

Our results do not support our previous hypothesis that sediment grain size controls species distribution, however, results do express that the influence of pore water salinity and nutrient composition modify forest structure, in local scale. Our data shows that the distance from the coast has a highly influence in a set of environmental variables (e.g. pore water salinity and nutrient availability), which may constrain species distribution. Species distributions reveal that mangrove structures are a result of species tolerance (e.g. tolerance to salinity and calcium and phosphorus soil content). Because those environmental factors vary in a local scale, the forest structure of each studied bay represent a specific set of species tolerance influenced by environmental variables.

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CAPÍTULO 3

ARE GAS EXCHANGE ADJUSTMENTS IN ORDER TO COPE WITH SOIL FEATURES AFFECTING MANGROVE ZONATION IN SOUTHERN BRAZIL?

Submetido ao periódico Aquatic Botany

Are gas exchange adjustments in order to cope with soil features affecting mangrove zonation in Southern Brazil?

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Abstract

The study measures leaf gas exchange parameters and abundance of stable isotopes of C and N of three mangrove species (*Rhizophora mangle* L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke and *Laguncularia racemosa* (L.) Gaertn) to investigate if photosynthetic capacity and water use efficiency constrain distribution and development of mangrove in the Guaratuba Bay Estuary, Brazil, around 25ºS. We measured gas exchange rates of three mangrove species in plots along an inundation gradient that differ in salinity. We used gas exchange parameters to calculate intrinsic water use efficiency (A_{max}/g_s, *WUEi*). Long-term water use efficiency was calculated based on $\delta^{13}C$ values, and $\delta^{15}N$ values were related to potential nutrient limitation. *Avicennia schaueriana* showed the capacity to maintain high *WUEi,* even with high g_s under higher salinities. The foliar $\delta^{13}C$ of *L. racemosa*, was lower than the other species and negatively correlated to pore-water salinity, which may explain the species distribution pattern. *Rhizophora mangle* gas exchange parameters did not correlate to the measured soil variables. Although the difference was not significant to *R. mangle*, the values indicate that fringe mangroves may use a marine source of ^{15}N. How species respond to changes in pore-water salinity is expressed in both gas exchange parameters and isotopic signature through the salinity gradient, which indicates that zonation may be related to species ecophysiological responses to salinity variations.

Key words: photosynthetic rates; stable isotopes; salinity tolerance; water use efficiency.

Introduction

Mangroves are defined as tree communities that occur in intertidal zones, essentially in tropical coastal areas (Tomlinson, 1986). Mangroves are highly connected to other ecosystems, representing a source of subsidies for fauna and also source of organic matter to adjacent communities (Feller et al., 2010). With worldwide distribution, mangroves occupy the Atlantic coast in the American continents, from 29º N to 29º S. Five species occur in Atlantic tropical southern areas but only three of these are able to occupy subtropical areas (Schaeffer-Novelli et al., 1990; Lüttge, 2008): *Rhizophora mangle* L., *Avicennia schaueriana* Stapf & Leechm. ex Moldenke. and *Laguncularia racemosa* (L.) Gaertn. Species distribution in subtropical mangroves are constrained by tolerance to freezing temperatures, to establishment of seedlings, and the development of saplings and trees (Schaeffer-Novelli et al., 2000; Kathiresan & Bingham, 2001; Kao et al., 2004; Krauss et al., 2008).

In the range of distribution of mangrove ecosystems, physiological differences drive alterations in forest species composition, structure, and function along environmental gradients (Ball, 1996; Krauss et al., 2008; Lima & Tognella, 2012). Physiological differences among species related to their tolerance of environmental conditions may play a part in mangrove species dominance and occurrence (Smith, 1992; Ball, 1996, 2002; Lüttge, 2008). Thus, each geographic zone shows a set of environmental features that results in forests with distinct physiognomies (Schaeffer-Novelli et al., 1990), since species occurrence and development may be affected by factors on a regional scale, e.g., water balance, wave regime and tides (Smith, 1992; Schaeffer-Novelli et al., 2000).

Previous studies showed distinct forest structure along the Brazilian coast (Carmo et al., 2000; Bernini & Rezende, 2004; Silva et al., 2005; Petri et al., 2011; Lima & Tognella, 2012). Based on that, Schaeffer-Novelli (1990) divided the coastline into eight units in a latitudinal range, which shows similar environmental conditions within each unit. We expect similar forest structures inside these latitudinal ranges as those delineated by Schaeffer-Novelli (1990). However, within a mangrove forest occupying the same geomorphological settings, species occurrence and development may also by controlled by the degree of soil saturation and topography, which determines tidal and fresh-water runoff, sediment composition, and stability (Tomlinson, 1986). These factors impact tree species differently and may result in a zonation pattern, such as those observed in southern Brazil. In southern Brazil, under the 25º S coordinate, mangroves presented distinct species distribution

(Sessegolo, 1997; Bigarella, 2001; Dornelles et al., 2006; Kilca et al., 2011; Madi et al., 2016). These distribution patterns may be influenced by the specific physiological tolerance of each species. However, ecophysiological studies that correlate structure and environmental conditions in Brazilian mangroves are insufficient to elucidate the absence or occurrence of zonation patterns in subtropical mangrove areas (Pascoalini et al., 2014; Soares et al., 2015).

Mangrove environments may characterize a physiological challenge for plants because of the salinity and, consequently, the highly negative water potentials of the soil pore water (Krauss et al., 2008; Cardona-Olarte et al., 2013). Therefore, the main issue to mangrove tree species is the tradeoff between water loss and carbon gain, since water acquisition is more energetically expensive than in non-saline soils (Reef & Lovelock, 2015). Ecophysiological parameters may reveal the ability of a plant to use water for biomass production, such as water use efficiency (*WUE*). Higher *WUE* may suggest a better competitive potential for the species by decreasing salt accumulation and water deficits at edge salinities (Krauss et al., 2006). Considering the importance of stomatal closure as the first event restricting photosynthesis at water stress (Flexas et al., 2004), the intrinsic water use efficiency (*WUEi,*), defined as the ratio between net CO_2 assimilation and stomatal conductance may represent how much biomass is produced for a given amount of water related to gas exchange occurring during photosynthesis process (Farquhar et al., 1982).

Despite the large representation of this parameter, *WUE* is estimated from leaf gas exchange, which makes it subject to temporal variance (Ferrio et al., 2003; Flexas et al., 2007). In order to avoid the effect of instantaneous measurements, *WUE* may also be estimated from stable carbon isotope composition ($\delta^{13}C$), which is a time-integrated physiological indicator. Its represent how much of the isotope ^{13}C, comparative to the amount of isotope ^{12}C, is discriminated in physicochemical process involved in leaf photosynthesis (Farquhar et al., 1989). Leaf $\delta^{13}C$ reveals time-integrated WUE established on a long time during leaf lifespan, while *WUEi* only reflects water use efficiency instantly, in the recording procedure throughout gas exchange measurements (Cao et al., 2012). Thus, environmental factors that impacts gas exchange components may reflect in $\delta^{13}C$ variation, e.g. a higher discrimination against the heavier C isotope indicates a higher average conductance over the lifespan of the leaves and lower soil water potential (Cheeseman & Lovelock, 2004), while less negative $\delta^{13}C$ values are correlated with higher water use efficiency (Medina & Francisco, 1997).

Although gas exchange characteristics of mangrove species have been explored considerably (Cintron et al., 1978; Clough & Sim, 1989; Lin & Sternberg, 1992a; Sobrado, 2000; Naidoo, 2010), the study of Soares et al. (2015) is, so far, the only ecophysiological research carried on the southernmost distribution of mangroves on the Atlantic coast, resulting in a lack of knowledge about how physiological tolerance impacts mangrove species distribution in subtropical areas. Their results suggest ecophysiological responses of species, e.g., low photosynthetic rates and values of carboxylation index as constraining factors to species distribution in higher latitudes, although they did not correlate their results with soil nutrient content.

Thus, this study aimed to investigate how photosynthetic capacity and water use efficiency constrain species distribution and development of mangrove in along an environmental gradient, in a Brazilian subtropical mangrove forest. We addressed the two following questions: Do leaf gas exchange parameters and isotopic signature of mangrove tree species differ among zones along the floodplain gradient? Also, are the ecophysiological responses to the environmental changes different among species? Overall, we hypothesized that differences gas exchange reflects photosynthetic capacity and differ among species, modulating differences in forest structure. For example, *A. schaueriana* seems to be more tolerant to salinity, thus, exhibiting higher stomatal conductance in fringe mangroves and individuals with pronounced development, even were pore water salinity is higher, such as fringe areas.

Methods

Site description

The Pinheiros River Estuary is located in the coast of Paraná State, Brazil, inside the Guaratuba Bay (between 25º50'S - 25º48'S and 48º34'W - 48º36'W). The climate is classified as *cfa* (mesothermal) in the Köppen system, with annual mean temperature of 20.8°C and annual rainfall of 3183mm during 2012. Since the estuary is located close to the mouth of Guaratuba Bay, the soil had higher porewater salinity and organic matter content than those further inland in the bay. The soil is characterized as salic-sodic thiomorphic gleysol.

Along the estuary, parallel to the river, nine 50m^2 plots were marked at different distances from the river, in order to represent the zonation pattern express by mangrove species. Plots were classified into physiographic types according to the simplified classification by Schaeffer-Novelli et al. (2000), altered by Estrada et al.

(2013): three fringe, three intermediary, and three interior plots. A previous study showed differences in forest structure of the Pinheiros River Estuary according to the above classification (Larcher et al., Unpublished results): *L. racemosa* has higher density and dominance in fringe, whereas *R. mangle* is the most representative species in interior plots. In intermediary plots, both species were codominant. *Avicennia schaueriana* has higher density in fringe, decreasing towards interior plots.

Abiotic factors

Salinity of pore-water was measured at low tide with a digital hydrometer (Akso AK83) in five randomly selected points within each plot, 30cm deep, during gas exchange measurements. Two samples of sediment from each plot were collected at low tide with an auger. To determine sediment nutrient composition, samples were collected at 10cm and 30cm depth. Particle-size distribution (30cm deep) was determined using a particle analyzer (Raij et al. 2001). Organic matter content (OM), pH values and soil cation exchange capacity (CEC) for the <2mm fraction were measured according to standard procedures as described in Camargo et al. (2009).

Photosynthetic gas exchange and leaf water potentials

Measurements of gas exchange were conducted in the summer of 2013/2014, between December and January. The number individuals *per* species measured depended on the frequency of species ranging from 2 to 5 individuals per species in each plot, with a total range for all plots varying from 2 to 14 individuals per species. Three sunlight exposed mature leaves were analyzed. Measurements were conducted from11:00 to 13:00 in sunny days (PAR > 1000 μmol m^{-2} s^{-1}), under natural humidity and temperature conditions.

We used a portable infrared gas analyzer open system (IRGA CI-340 model, BioScience), which performs measurements of CO_2 concentration, temperature, relative humidity and PAR. From these parameters, considering the approximate atmospheric CO_2 concentration of 380μmol mol^{-1}, assimilation rate (A, μmol $m^{-2}s^{-1}$), stomatal conductance stomatal (g_s, mol $m^{-2}s^{-1}$), and internal CO_2 concentration (Ci ppm) were calculated. Assimilation in these species was light saturated at 1000 μmol m^{-2} s^{-1}, thus measured rates at this level of light were designated as A_{max} . We calculated the intrinsic water use efficiency (*WUEi*, mmol CO_2 mol^{-1} H_2O) as the ratio A_{max}/g_s (Farquhar et al. 1982) and A_{max}/C_i ratio was used as carboxylation efficiency index (*CE*) (Kiran et al. 2013).

Isotope Analysis

Leaf samples from the same individuals were collected just after measuring gas exchange parameters for isotopic analyses. Leaves were dried at approximately 60°C and ground for the analysis of stables isotopes of C and N, expressed in delta units ($\delta^{13}C$ and $\delta^{15}N$). These analyses were conducted at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems (University of Miami, EUA) using a CN-analyzer (Euro-EA-Elemental Analyser, Eurovector, Milan, Italy) connected to a mass spectrometer (Elementar, Germany) to measure the isotopic natural abundance. The $\delta^{13}C$ values are indicative of the long-term leaf water use efficiency (Farquhar et al. 1982) and $\delta^{15}N$ values represent origin and availability of N in soils (Fry et al. 2000).

Data analysis

Means (± standard error of mean) were calculated for all quantitative variables. We performed a one-way analysis of variance (ANOVA) grouping by species and plots. Differences of soil parameters among plots were also tested with ANOVA. Post-hoc Tukey's tests were performed as pairwise comparison tests. We used linear regressions to test the effect of soil parameters (organic matter content, pH, cation exchange capacity, sand content and pore-water salinity) on gas exchange (*WUEi*, A_{max}) and isotopic signature ($\delta^{13}C$ e $\delta^{15}N$) of species. ANOVA, Tukey and regressions were performed with R (v2.15.2; R foundation for statistical computing, Vienna, Austria).

Results

Abiotic factors

There were no differences among the sediment traits of fringe, intermediary, and interior plots at Guaratuba Bay, except for pore-water salinity (Welch's *ANOVA*, F=9.27, p<0.0001, Table 1). Fringe plots presented the highest pore-water salinity while interior plots presented the lowest. Intermediary plots presented pore-water salinity intermediate to fringe and interior plots and was not significantly different to both types of plots. Particle-size distribution analysis did not show differences among areas. All plots presented the following content of particle size distribution: sand>silt>clay.

Table 3-1: Mean values (± standard deviation) of pore-water salinity (Salinity, ‰), organic matter content (OM, 10 cm deep, $g.dm^{-3}$), pH, phosphorus content (P, 10 cm deep, $mmol.dm^{-3}$) and particle size content (fines sediment and sand, %) from sediments at the Guaratuba Bay (Brazil). Within column numbers followed by the same letter are not statistically different (p=0.05).

	Salinity	OM	pH	P	CEC	Fines	Sand
Fringe	22±1.5 a	84±7	5.1±0.3	10.4±1.4	203.4±27	62±8	37±8.1
Intermediary	20±1.9 ab	94±20	5.1±0.2	9.0±1.3	204.4±36	55±4	45±4.0
Interior	19±0.2 b	104±17	5.1±0.1	10.0±2.1	201.3±37	52±4	47±4.2
n	15	8	8	8	8	8	8
Welch's *ANOVA*	<0.001, *F*=9.27	0.58	0.56	0.58	0.66	0.76	0.58

Photosynthetic gas exchange and leaf water potentials

The three mangrove species showed different variation in measured parameters between fringe, intermediary and interior plots (Table 2). *Rhizophora mangle* individuals showed similar T_{leaf}, *Ci*, *gs* and A_{max} among plots, but *E* was higher in interior plots and lower in intermediary plots. *A. schaueriana*, had similar values of T_{leaf}, *Ci*, *T* and A_{max}, while *gs* values were higher in fringe plots and lower in interior plots. *Laguncularia racemosa* showed variation in T_{leaf}, with higher values in fringe and intermediary plots, and higher A_{max} in fringe and lower in intermediary plots.

Laguncularia racemosa showed lower *WUEi* than *R. mangle* and *A. schaueriana* (ANOVA, F=4.38, p<0.01), however, *WUEi* was similar among plots for all species (Table 3). There is a significant correlation between *WUEi* and *CE* (Figure 1), but regression differed among the species. The increase in *CE* with *WUEi* variation was correlated in *R. mangle* (R^2=0.582, F=58.1, p<0.01, slope = 0.00068) and *A. schaueriana* (R^2=0.563, F=24.5, p<0.0001, slope = 0.00044), and strongly correlated in *L. racemosa* (R^2=0.755, F=108.1, p<0.0001, slope = 0.00044). The correlations among gas exchange and soil parameters also differ among species (Table 4). *WUEi* and A_{max} of *A. schaueriana* and *R. mangle* were not correlated to

soil parameter. In *L. racemosa* leaves, *WUEi* and A_{max} were positively correlated to pH; A_{max} was also correlated negatively to OM.

Table 3-2: Gas-exchange parameters per species by zones in the floodplain gradient of the Guaratuba Bay Mangrove Forest (Brazil). Mean values (± standard error of mean), number of analyzed individuals (*n*), Light intensity (Q_L, μmol.m^{-2}.s^{-1}), leaf temperature (T_{Leaf}, ºC), intercellular CO_2 concentration (C_i, ppm), transpiration rate (*E*, mmol.m^{-2}.s^{-1}), stomatal conductance (g_s, mol.m^{-2}.s^{-1}), and light-saturated photosynthetic rate (A_{max}, μmol.m^{-2}.s^{-1}). Within column numbers followed by the same letter are not statistically different (*p*=0.05).

Site	*n*	Q_L	T_{Leaf}	C_i	*E*	g_s	A_{max}	*CE*
	Avicennia schaueriana							
Fringe	13	2053 ± 152	38.3 ± 0.7	273 ± 5	3.38 ± 0.18	0.12 ± 0.01a	6.55 ± 0.56	0.024 ±0.002a
Intermediary	6	1909 ± 276	39.1 ± 1.7	263 ± 10	3.38 ± 0.41	0.11 ± 0.01ab	6.09 ± 0.74	0.023 ± 0.003a
Interior	2	1612	41.1	269	2.82	0.07	3.40	0.013b
ANOVA		p=0.42	p=0.17	p=0.54	p=0.62	*F*=6.8, p<0.01	p=0.12	*F*=3.45, p<0.05
	Laguncularia racemosa							
Fringe	14	2067 ± 149	37.7 ± 0.7b	308 ± 3	3.47 ± 0.29	0.14 ± 0.01	6.90 ± 0.86a	0.022 ± 0.003a
Intermediary	13	2220 ± 100	41.1 ± 0.4a	306 ± 4	3.91 ± 0.25	0.11 ± 0.01	4.18 ± 0.48b	0.014 ± 0.001b
Interior	10	2175 ± 160	39.9 ± 1.1a	291 ± 7	3.78 ± 0.37	0.12 ± 0.01	5.37 ± 0.68ab	0.018 ± 0.002ab
ANOVA		p=0.79	*F*=7.6, p<0.05	p=0.20	p=0.55	p=0.25	*F*=4.1, p<0.05	*F*=3.97, p<0.02
	Rhizophora mangle							
Fringe	14	2208 ± 148	41.0 ± 0.5	284 ± 4	3.99 ± 0.18ab	0.12 ± 0.01	5.68 ± 0.46	0.020 ± 0.002
Intermediary	11	2051 ± 157	40.2 ± 0.4	284 ± 6	3.29 ± 0.25b	0.10 ± 0.01	5.41 ± 0.55	0.019 ± 0.002
Interior	13	2341 ± 152	41.9 ± 0.9	275 ± 5	4.31 ± 0.36a	0.11 ± 0.01	5.28 ± 0.41	0.019 ± 0.003
ANOVA		p=0.39	p=0.33	p=0.39	*F*=3.4, p<0.05	p=0.28	p=0.82	p=0.89

Table 3-3: Mean values (± standard deviation) of Intrinsic water-use efficiency (WUE_i, $mmol.mol^{-1}$) and isotopic signature per species by zones in the floodplain gradient of the Guaratuba Bay Mangrove Forest (Brazil). Leaf carbon concentration (C,%), leaf nitrogen concentration (N,%), leaf isotopic abundance of ^{13}C ($\delta^{13}C$, ‰) and ^{15}N ($\delta^{15}N$, ‰). Within column numbers followed by the same letter are not statistically different (p=0.05).

Site	WUE_i	C	N	$\delta^{13}C$	$\delta^{15}N$
Avicennia schaueriana					
Fringe	52.32 ± 2.77	42.51 ± 0.76	2.26 ± 0.13	-28.52 ± 0.29	4.04 ± 0.43a
Intermediary	57.19 ± 7.95	41.69 ± 1.03	1.79 ± 0.16	-27.95 ± 0.59	1.43 ± 0.21c
Interior	49.65 ± 0.37	43.88 ± 0.56	2.26 ± 0.50	-28.26 ± 0.50	2.16 ± 0.35b
ANOVA	p=0.69	p=0.58	p=0.13	p=0.61	F=8.91, p<0.01
Laguncularia racemosa					
Fringe	49.09 ± 5.81	43.52 ± 0.42	1.12 ± 0.07	-30.60 ± 0.17b	3.04 ± 0.40a
Intermediary	37.25 ± 3.68	42.42 ± 0.22	0.97 ± 0.03	-30.47 ± 0.24b	0.48 ± 0.20b
Interior	42.54 ± 3.99	43.44 ± 0.44	1.14 ± 0.08	-29.55 ± 0.41a	0.88 ± 0.45b
ANOVA	p=0.20	p=0.06	p=0.11	F=4.2, p<0.01	F=16.12, p<0.01
Rhizophora mangle					
Fringe	48.70 ± 2.36	45.24 ± 0.37	1.64 ± 0.06	-29.12 ± 0.27	2.29 ± 0.57
Intermediary	54.94 ± 3.22	45.94 ± 0.43	1.69 ± 0.07	-29.12 ± 0.36	1.33 ± 0.10
Interior	48.22 ± 3.24	46.18 ± 0.45	1.69 ± 0.04	-28.62 ± 0.31	1.51 ± 0.47
ANOVA	p=0.23	p=0.24	p=0.80	p=0.42	p=0.29

Table 3-4: Correlation coefficients for gas exchange and isotopic signature of leaves and soil properties of *Avicennia schaueriana* (A), *Laguncularia racemosa* (B) and *Rhizophora mangle* (C). Bold numbers reflect significant correlations ($p<0.05$). Negative signs imply inverse correlation. Dark gray shaded cells reflect correlation between physiological and abiotic characteristics. Light gray shaded cells reflect possible auto-correlations between parameters.

(A)	$\delta^{13}C$	$\delta^{15}N$	*WUEi*	A_{max}	OM	pH	CEC	Sand
$\delta^{13}C$	1.00							
$\delta^{15}N$	-0.10	1.00						
WUEi	0.14	-0.07	1.00					
A_{max}	-0.11	0.09	0.70	1.00				
OM	-0.07	-0.40	0.17	-0.20	1.00			
pH	0.10	0.14	-0.34	-0.28	-0.28	1.00		
CEC	-0.29	0.00	-0.01	-0.17	0.83	-0.17	1.00	
Sand	0.18	-0.55	0.25	0.06	-0.02	-0.29	-0.49	1.00
PWSalinity	-0.28	0.61	-0.08	0.15	-0.11	0.25	0.39	-0.92
(B)	$\delta^{13}C$	$\delta^{15}N$	*WUEi*	A_{max}	OM	pH	CEC	Sand
$\delta^{13}C$	1.00							
$\delta^{15}N$	-0.11	1.00						
WUEi	-0.26	0.27	1.00					
A_{max}	-0.31	0.37	0.88	1.00				
OM	0.23	-0.23	-0.29	-0.41	1.00			
pH	0.06	0.26	0.41	0.43	-0.57	1.00		
CEC	0.11	0.19	-0.12	-0.22	0.87	-0.53	1.00	
Sand	0.18	-0.46	-0.31	-0.34	-0.26	0.06	-0.56	1.00
PWSalinity	-0.32	0.47	0.24	0.28	-0.25	0.37	0.02	-0.38
(C)	$\delta^{13}C$	$\delta^{15}N$	*WUEi*	A_{max}	OM	pH	CEC	Sand
$\delta^{13}C$	1.00							
$\delta^{15}N$	-0.15	1.00						
WUEi	0.04	-0.14	1.00					
A_{max}	0.11	0.04	0.56	1.00				
OM	-0.11	0.27	0.03	-0.09	1.00			
pH	0.15	-0.24	0.27	0.23	-0.60	1.00		
CEC	-0.23	0.49	-0.05	-0.12	0.86	-0.56	1.00	
Sand	0.26	-0.70	0.27	0.05	-0.28	0.19	-0.59	1.00
PWSalinity	-0.21	0.04	0.30	0.30	-0.40	0.49	-0.16	-0.25

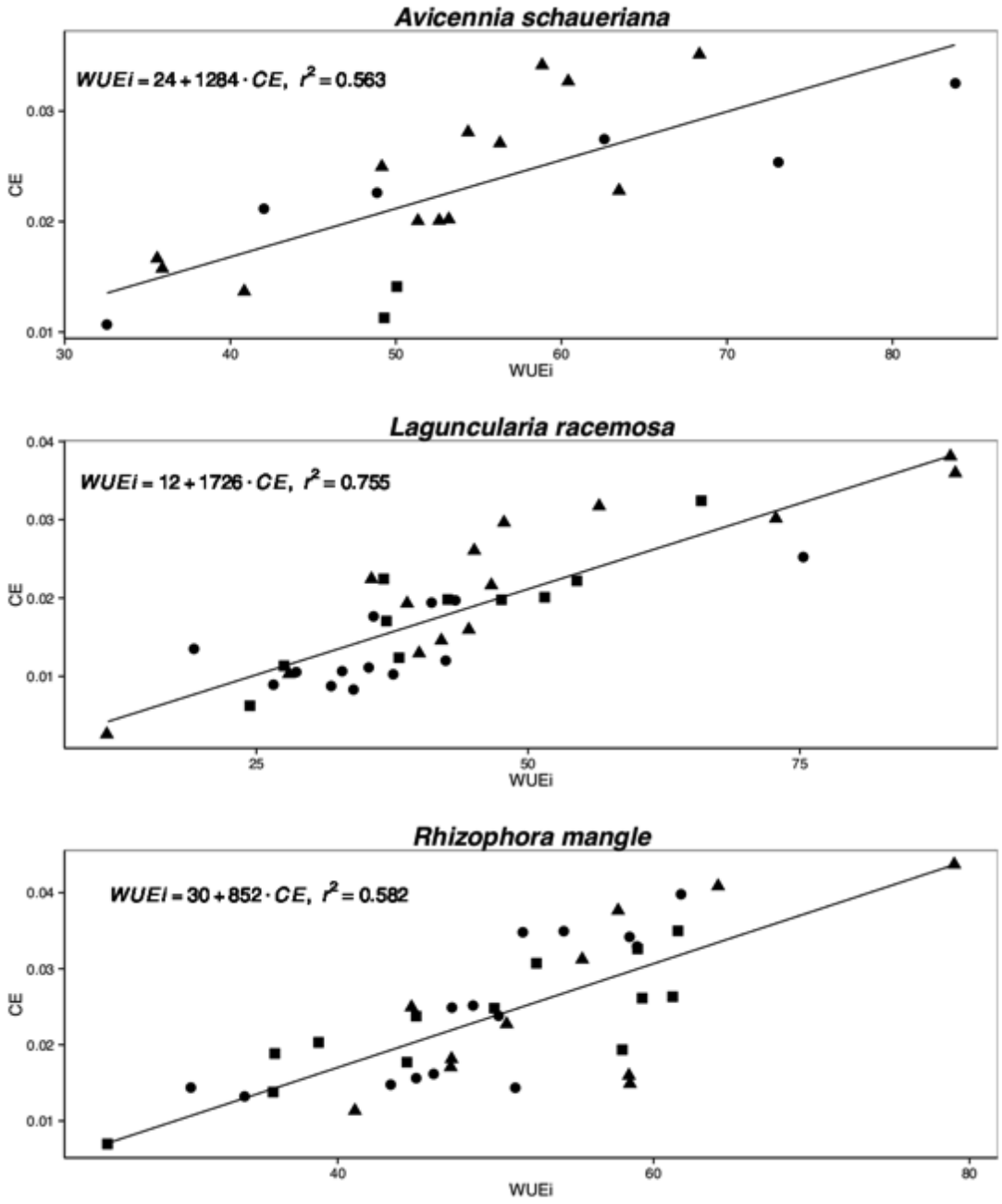

Figure 3-1: Regressions of carboxylation efficiency (CE) versus intrinsic water-use efficiency (*WUEi*). Black triangles: fringe plots; Black circles: Intermediary plots, Black squares: Interior plots.

Isotope analysis

Avicennia schaueriana exhibited lower *%C* and higher *%N* in all plots, compared to the other species. The foliar carbon and nitrogen isotopic ratios of R. mangle were similar among plots, while *A. schaueriana* individuals presented higher $\delta^{15}N$ in fringe plots (Table 3). *Laguncularia racemosa* displayed both more negative

$\delta^{13}C$ and higher $\delta^{15}N$ values in fringe plots. Despite some differences among species, we found that all species tended to have a higher $\delta^{15}N$ value in the fringe plots. $\delta^{13}C$ values were similar between *A. schaueriana* and *R. mangle* and lower in *L. racemosa*, but all values were in the range between -27.95‰ and -30.60‰ (Figure 2).

The correlations among isotopic signature and soil parameters differ among species (Table 4). $\delta^{13}C$ of *L. racemosa* leaves were negatively correlated to pore-water salinity while $\delta^{15}N$ was correlated negatively to sand content in all species. $\delta^{15}N$ was positively correlated to pore-water salinity in *L. racemosa* and *A. schaueriana* and positively correlated to CEC in *R. mangle*.

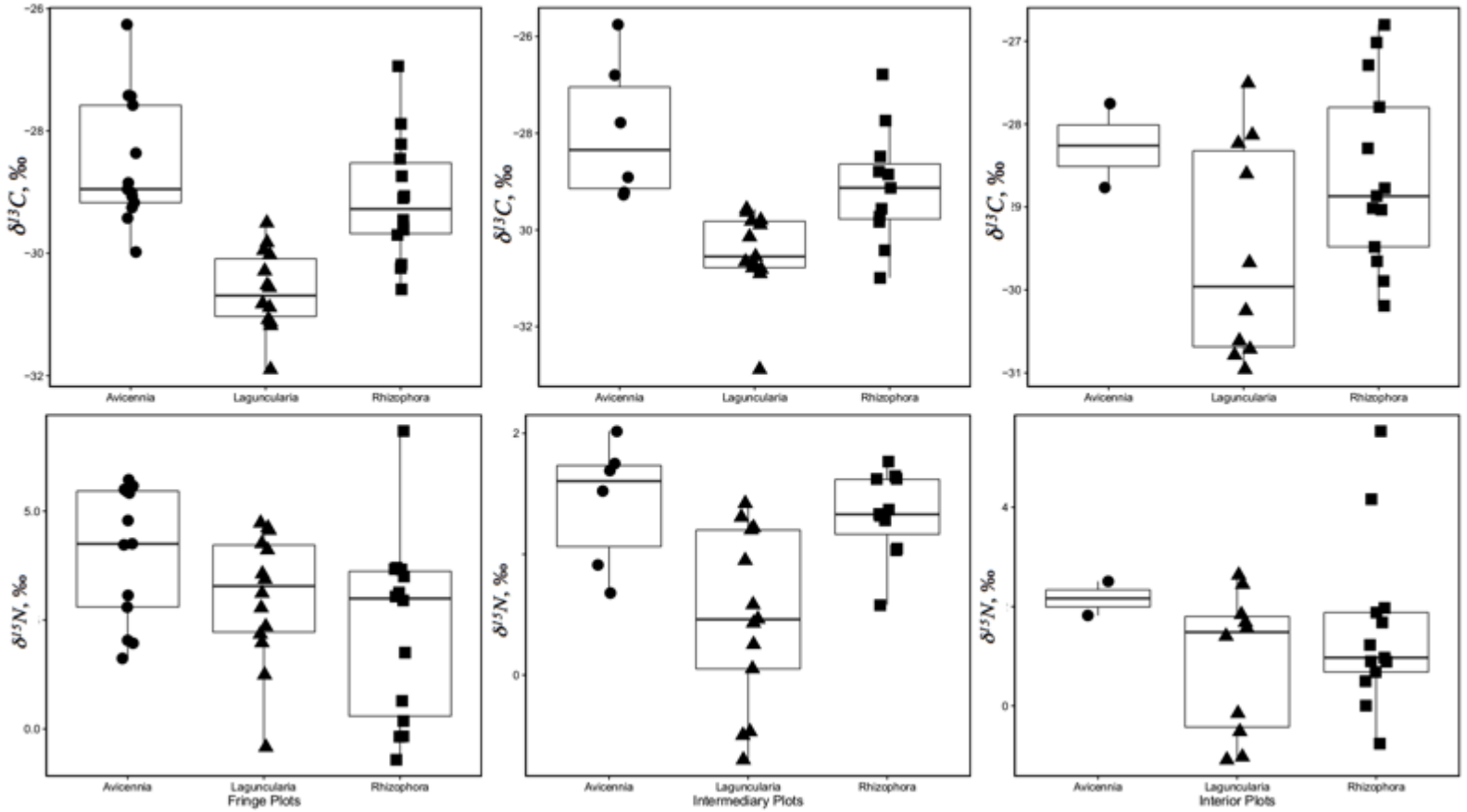

Figure 3-2: Isotopic ratios of *Avicennia schaueriana* (A), *Laguncularia racemosa* (L), *Rhizophora mangle* (R). 13C: leaf isotopic abundance of ^{13}C ($\delta^{13}C$, ‰), DelN: leaf isotopic abundance of ^{15}N ($\delta^{15}N$, ‰); A, B: fringe plots; C, D: Intermediary plots, E, F: Interior plots.

Discussion

Salinity seems to be the main factor differentiating mangrove soil and forest structure, as previous found by other studies (Lovelock and Feller 2003; Lovelock et al. 2006a; Krauss et al. 2008; Parida and Jha 2010). Despite some differences in species performance among plots, such as photosynthetic rate in *L. racemosa* leaves, g_s in *A. schaueriana* leaves and *E* in *R. mangle* leaves, the distinction was higher among species than among plots for each species, which may be associated to the range of tolerance of species. Previous studies indicate a trend of tolerance to salinity in this order: *Avicennia* > *Laguncularia* > *Rhizophora* (Sobrado 2000, Lovelock and Feller 2003, Sobrado and Ewe 2006, Lugo et al. 2007, Lüttge 2008, Da Cruz et al. 2013, Soares et al. 2015, among others). These authors suggest that *R. mangle* and *L. racemosa* have narrower salt-tolerances than *Avicennia* species, because of their limited ability to cope with water and salt uptake balance. In our results, the three species showed little variation in gas exchange parameters, e.g. A_{max} and g_s. However, *WUEi* and isotopic signature of species showed that *R. mangle* and *L. racemosa* have a narrower range of salinity.

Among plots, *A. schaueriana* leaves of fringe plots exhibited higher g_s in fringe plots than in intermediary and interior plots, showing that species present physiological adjustments to maintain high productivity in high salinity areas. The carbon incorporation in mangrove species represents a tradeoff between water loss and carbon gain. To increase carbon gain, species must increase gas exchange, however, the water loss through the gas exchange can make carbon acquisition expensive (Lüttge 2008). Those species that can maintain great carbon incorporation with considerable gas exchange in salinity environments have higher carboxylation efficiency.

Avicennia schaueriana and *R. mangle* showed no differences in both short (*WUEi*) and long-term ($\delta^{13}C$) water use efficiency. *Rhizophora mangle* have the highest slope of correlation between *WUEi* and *CE.* Soares et al (2015) found distinctive results and suggests that the low values of *CE* by *R. mangle* might be a physiological limitation to species establishment in costal areas with subtropical climate conditions. However, in our study, *R. mangle CE* does not vary among plots. Therefore, it is not possible to affirm that *R. mangle* is less competitive in salinity conditions.

In addition, *R. mangle* presented higher values of *E* both in interior and fringe plots. High *E* may indicate a lower impact of salinity and the ability to deal with water loss and maintain adequate carbon gain. Indeed, neither transpiration nor other gas

exchange parameters of *R. mangle* were correlated to the abiotic studied variables. Other factors as differences among xylem tension to soil salinity, propagules survival, biotic interactions and other external abiotic factors may be related to *R. mangle* occurrence. Lin and Sternberg (1992) found no variation in A_{max} and g_s between fringe and scrubs *R. mangle* in Florida, though indicate the salinity fluctuation may have significant effects on growth and distribution mangroves. In fact, Sobrado (2000) indicate that the lower transport efficiency due to wood characteristics associated to the conservative water use found in *L. racemosa* and *Avicennia germinans* L. may have advantages in the zones with high and fluctuating salinities. *Rhizophora mangle* may not be well adapted to salinity in areas where salinity changes fast, which may explain its distribution in the study areas.

Laguncularia racemosa showed greater A_{max} relative to the other two species. Also, A_{max} was higher in both fringe and interior plots than in intermediary plots, which does not explain the species zonation in the study area. On the other hand, while there is no difference in *WUEi* among zones, which indicates similar short-term water use efficiency, $\delta^{13}C$ significantly shifted to a higher value in interior plots, suggesting higher long-term water use efficiency probably caused by higher stress. The lower discrimination against C isotopes and consequently higher $\delta^{13}C$ indicates a more restricted CO_2 source often caused by lower conductance over the lifespan of the leaves (Cheeseman and Lovelock 2004). In *L. racemosa*, $\delta^{13}C$ was negatively correlated to pore-water salinity, which may indicate a narrower range of salinity tolerance and, consequently, explain the species distribution pattern found in this study.

Despite the absence of significant differences among plots*, WUEi* in *L. racemosa* was positively correlated to pH, as well as A_{max}. Acidic soils with high CEC and organic carbon concentrations were previous linked to *Laguncularia* greater abundance (Lacerda et al. 1995; Lima and Tognella 2012; Urrego et al. 2014). Low values of pH, as found in this study, may impact nutrient availability (Krauss et al. 2008; Lima and Tognella 2012), however, salinity affects soil pH and it is very unlike to define solo effects. Salinity, pH and, consequently, nutrient stress affect the intrinsic photosynthetic capacity of *L. racemosa.*

The three species presented slightly lower A_{max} than previous reported by other studies in tropical and subtropical areas (Table 5). While species tend to present higher values of photosynthetic rate in tropical areas, we did not expect differences between our results and mangroves of high latitude in Brazilian areas. The range of photosynthetic rates reported by Soares et al (2015) to *A. schaueriana*, *L. racemosa* and *R. mangle* is higher than what we found in this study. However, two

factors can be highlighted: the geographic location of areas and the light intensity at measurements time. While Guaratuba Bay has a strait connection to Atlantic Ocean, the areas explored by Soares et al (2015) are located at the inner portion of the Tavares River Estuary, connected to the inland portion of the littoral. On the other hand, light intensity and leaf temperature at the time of measurements in our study was higher than found by Soares et al (2015), which may indicate photoinhibition processes. Lüttge (2008) suggests that salinity and irradiance stresses may be additive. Light intensity during measurements were over 1900 $\mu mol.m^{-2}.s^{-1}$, except for *A. schaueriana* leaves in interior areas, which may have lead to higher leaf temperature when compared to findings of Soares et al (2015). Nandy and Ghose (2007) indicate that photosynthesis start to decrease as leaf temperature exceeds 33-36º in *Avicenniaceae* and *Rhizophoraceae* species. We found higher leaf temperatures, which may explain the lower values of photosynthetic rates presented here by these mangrove species.

In plants under full sunlight, photosynthesis becomes light saturated due to the excess of excitation energy produced and photoinhibition occurs after a saturation point (Lüttge 2008). This performance is generally not expected in mangrove species because of the high physiological resistance against photoinhibition (Cheeseman et al. 1997; Nandy et al. 2007; Lüttge 2008). Although mangroves leaf chloroplasts are protected against chronic photoinhibition, it does not guarantee that acute photoinhibition will not happen. Previous studies indicates that, in order to cope with high insulation, mangrove species tend to dissipated the excess of energy mainly by heat, which may also decrease photosynthesis (Cheeseman et al. 1997; Data and Ghose 2005; Sobrado 2005; Alongi et al. 2005).

In spite of salinity and light effects on mangroves gas exchange and carbon fixation, it has been hypothesized that nutrient limitation may also determine carbon gain and, consequently, structural development and distribution in mangrove forests. The salinity effect on the inundation gradient may result in distinct nutrient content along the floodplain. Fry et al (2000) stated that the $\delta^{15}N$ signature of *R. mangle* varies due to changes in source of $\delta^{15}N$ and to differences in physiological fractionation, related to different plant stress level. The $\delta^{15}N$ of studied species may indicate differences in source of ^{15}N among plots: all three species showed higher values of $\delta^{15}N$ in fringe plots. Although the difference was not significant to *R. mangle*, the values indicate that fringe mangroves may use a marine source of ^{15}N. Trees from fringe are able to acquire inorganic N from sponges encrusting roots submerged in the tidal creek, which result in more positive signature (McKee et al. 2002). Also, under lower salinity, intermediary and interior plots may have higher

availability of N, which result in great fractioning and lower plant $\delta^{15}N$ towards inland (McKee et al. 2002).

Our findings that these species differed in their physiological response in relation to distance to the coast might explain their zonation. *Avicennia schaueriana* is more tolerant to salinity due to its capacity to maintain high WUEi, even with great conductance. While *L. racemosa*, $\delta^{13}C$ was negatively correlated to pore-water salinity, which may explain the species distribution pattern found in this study. *Rhizophora mangle* gas exchange parameters were little correlated to the studied soil variables and other factors may interfere in species distribution, such as tolerance to salinity variation. All three species were affected by salinity, but the degree of tolerance of each one may explain the zonation pattern founded in the Guaratuba Bay Estuary.

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CAPÍTULO 4

UMA REVISÃO SOBRE MANGUEZAIS NO BRASIL: A RELAÇÃO ENTRE ESTRUTURA DE FLORESTA E VARIAÇÕES AMBIENTAIS

Essays & Perspectives

Uma revisão sobre manguezais no Brasil: a relação entre estrutura de floresta e variações ambientais

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Palavras-chave: levantamentos fitossociológicos, estrutura de manguezal, escala ambiental, metodologia, mangue.

Resumo

Apesar de haver diversos levantamentos sobre a estrutura dos manguezais na costa brasileira, não há definição acurada sobre a relação entre estrutura/ desenvolvimento/ variáveis ambientais. Levantamentos fitossociológicos em áreas de manguezais, de 2000 a 2015, foram compilados afim de verificar se estes representam os padrões regionais na estrutura dos manguezais ao longo da costa brasileira e se os dados existentes são suficientes para estabelecer a relação entre variáveis ambientais e estrutura destes manguezais. Os levantamentos sugerem que a composição e o desenvolvimento das florestas de manguezal variam em escala local, tendo características intrínsecas de cada floresta. Fatores como salinidade, dinâmica de marés, competição interespecífica e grau de impacto ambiental são apontados como atuantes na configuração atual das florestas de mangue. Apesar de caracterizar a estrutura das comunidades, os estudos não definiram os processos que influenciam a estrutura de cada manguezal. Investigações que avaliem quantitativamente as características ecofisiológicas das espécies, parâmetros físico-químicos dos ambientes associados à estrutura das florestas e parâmetros em diferentes escalas temporais e espaciais podem auxiliar na interpretação dos processos que ao longo do tempo definiram os padrões estruturais atualmente encontrados.

Introdução

Investigações que abordem a estrutura das florestas de manguezais são importantes para o estabelecimento de medidas de manejo e sustentabilidade de áreas costeiras, baseado na variação das respostas dos manguezais às alterações ambientais e sua importância ecológica para os ambientes adjacentes (Soares 1999; Schaeffer-Novelli et al. 2000; Godoy & Lacerda 2015). Embora a diversidade de espécies arbóreas ocorrentes nos manguezais seja reduzida quando comparada com outras florestas tropicais, a grande interação dos fatores abióticos influenciando a ocorrência e o desenvolvimento dessas espécies resulta em manguezais com estruturas diferentes ao longo da costa brasileira (Schaeffer-Novelli et al. 1990; Kathiresan & Bingham 2001; Soares et al. 2012).

Padrões de distribuição das espécies de mangue são relatados desde os primeiros estudos ecossistêmicos (Lugo & Snedaker 1974; Cintron & Novelli 1984; Bigarella 2001). Apesar dos inúmeros levantamentos sobre a estrutura, as metodologias divergentes adotadas dificultam a comparação de resultados e uma definição mais acurada da relação estrutura/desenvolvimento/variáveis ambientais. Portanto, este estudo compilou levantamentos fitossociológicos em áreas de manguezais, de 2000 à 2015, afim de responder as seguintes questões: Os levantamentos representam padrões regionais na estrutura dos manguezais ao longo da costa brasileira? Os dados existentes são suficientes para estabelecer a relação variáveis ambientais/estrutura destes manguezais?

Apesar de caracterizar a estrutura das comunidades ao longo da costa brasileira, os estudos não definiram os processos que influenciam a estrutura de cada manguezal. A investigação de componentes específicos, como respostas à variações nos fatores abióticos e bióticos, pode elucidar os processos que resultaram nos padrões estruturais atualmente encontrados.

Métodos

Para este estudo, foram considerados artigos publicados entre os anos de 2000 e 2015, utilizando ferramentas de busca online em bases de dados acadêmicos. Os termos de busca foram: fitossociologia, florística, floresta, estrutura, distribuição, manguezal, mangue e árvores de mangue.

Entre os artigos encontrados, 23 foram selecionados, distribuídos ao longo da costa brasileira. Estes estudos foram padronizados pelo uso do método de

parcelas para o levantamento da estrutura da comunidade arbórea (Tabela 1), com exceção do artigo de Matni et al. (2006) que utilizou o método do quadrante centrado, mas permitiu a comparação entre escalas ambientais. Não foi possível padronizar o critério de inclusão dos indivíduos, devido a grande divergência entre os estudos. Três estudos na Região Norte, seis na Região Nordeste, nove na Região Sudeste e cinco na Região Sul do Brasil foram selecionados.

Estrutura das florestas de manguezal no Brasil

Os estudos fitossociológicos dos manguezais brasileiros apontaram a ocorrência de quatro espécies arbóreas, com distribuição diferenciada: *Laguncularia racemosa e Rhizophora mangle* ocorrem desde o Rio Oiapoque (AP) até a Ilha de Santa Catarina (SC). *Avicennia germinans* ocorre desde da Região Norte até a desembocadura do Rio Macaé (RJ) e *A. schaueriana* é associada às Regiões Sudeste e Sul.

Na Região Norte, os levantamentos recentes estão, em sua maioria, localizados na Península de Ajuruteua, Bragança - PA (Silva & Fernandes 2004; Abreu et al. 2006; Seixas et al. 2006; Da Cruz et al. 2013). Esses bosques apresentam grande variabilidade fitoespacial, com manguezais sob condições distintas, o que justifica o grande esforço amostral nesta região (Matni et al. 2006). A distribuição e o desenvolvimento das espécies nestes manguezais são influenciados por interações bióticas, como competição (Silva & Fernandes 2004; Seixas et al. 2006) e abióticas, como salinidade e o aporte de água doce (Matni et al. 2006). Estudos em outras áreas do litoral Norte descrevem manguezais com estrutura semelhante à encontrada na península bragantina (Matni et al. 2006), suportando o padrão descrito para a região.

Na Região Nordeste, os estudos variaram em tamanho das parcelas analisadas, critérios de inclusão e escala ambiental, abordando subsistemas estuarinos (Soares et al. 2008), comparando estuários (Camargo Maia & Coutinho 2012) e manguezais em escala local (Paraguassu & da Silva 2007). Apesar de não serem comparáveis, todos os levantamentos citam a influência das atividades antrópicas nos manguezais, ressaltando a importância destes estudos para a conservação e manejo destas áreas.

A Região Sudeste concentra a maior área de ocupação urbana próxima à linha da costa (Schaeffer-Novelli et al. 2000), o que justifica o maior número de levantamentos encontrados. Esses estudos adicionaram o efeito de diferentes

tensores às variações ambientais, descrevendo, portanto, áreas com características estruturais e funcionais específicas (Soares et al. 2003). Os estudos existentes apontaram a importância de fatores abióticos como o regime de inundação e a salinidade da água intersticial (Bernini et al. 2014; Calegario et al. 2015), além do grau de conservação das unidades amostradas (Pereira et al. 2009; Petri et al. 2011). Entretanto, poucos estudos abordaram de forma quantitativa os aspectos abióticos e bióticos que influenciam a comunidade arbórea dos manguezais (Soares et al. 2003; Calegario et al. 2015).

A Região Sul é importante para o entendimento da ecologia dos manguezais por ser o limite de ocorrência deste ecossistema no Brasil (Schaeffer-Novelli et al. 2000; Soares et al. 2012), provavelmente pela ocorrência de baixas temperaturas durante o inverno e substituição dos manguezais por vegetação de marismas, devido as características da costa nesta região (Schaeffer-Novelli et al. 1990; Lima & Tognella 2012). Os estudos recentes em manguezais sul brasileiros apontam a superficialidade das pesquisas em elencar os processos que limitam a distribuição austral dos manguezais. Apesar da pequena extensão ocupada pelos manguezais nesta região, os resultados encontrados são divergentes quanto a estrutura e zonação. No entanto, os estudos são unânimes em sugerir a influência da salinidade na densidade e distribuição das espécies. Apesar de ainda não apresentarem alto grau de degradação, já existem registros de pressões antrópicas causadas pela expansão urbana nesta região, como a construção de portos e a indústria de lazer (Madi et al., no prelo).

A ocorrência e estrutura das florestas de manguezais são definidas por fatores que atuam em diferentes níveis hierárquicos de organização espacial (Soares et al. 2012). Poucos estudos de manguezais abordam áreas em diferentes escalas, o que dificulta o entendimento à respeito dos processos e fatores que interferem na ocorrência e distribuição das espécies. Em escala local, a estrutura da floresta é basicamente controlada pela frequência de inundação, a qual é determinada pela topografia e aporte de água doce (Lugo & Snedaker 1974; Estrada et al. 2013). Contudo, fatores bióticos, como predação e competição por luz e espaço, também determinam o desenvolvimento destas comunidades (Lima & Tognella 2012) e formam um complexo de fatores que, invariavelmente, são dependentes entre si.

Na Região Norte, numa escala local, a distribuição as espécies relaciona-se com a competição entre indivíduos ou interações bióticas, com pouca influência de fatores abióticos (Silva & Fernandes 2004; Seixas et al. 2006). Entretanto, a

salinidade e a frequência de inundação parecem ser os principais fatores influenciando a estrutura das florestas, em uma escala mais ampla (Matni et al. 2006).

Na Região Sul, apesar de visualizarem a estrutura da floresta em escalas diferentes, os resultados demonstraram a influência da dinâmica de maré e salinidade na distribuição das espécies. A salinidade da água intersticial parece influenciar a distribuição das espécies em escala regional (Madi et al. no prelo). Entretanto, em escala local, o efeito da tolerância à salinidade gera padrões de zonação diferenciados, mesmo em manguezais geograficamente próximos (Larcher, comunicação pessoal).

Metodologia dos estudos fitossociológicos

Apesar do método de parcelas múltiplas ser o mais difundido entre os estudos de manguezais (Soares 1999; Bernini & Rezende 2004; Silva et al. 2005), o tamanho (100 à 650 m^2) e o número de parcelas foi bastante variado. A variação desta metodologia indica a grande variabilidade na estrutura dos manguezais, mesmo em áreas geograficamente próximas.

Além disso, levantamentos que incluem todos os indivíduos dificultam a quantificação de parâmetros fitossociológicos, uma vez que indivíduos jovens e adultos são tratados igualmente. Indivíduos jovens podem apresentar respostas diferentes aos fatores abióticos (Madi et al. no prelo). É importante utilizar critérios que possam ser comparados entre populações e entre áreas geográficas distintas. Baseados nos resultados encontrados, ainda não é possível avaliar se as afirmações sobre o desenvolvimento e estrutura dos manguezais estão sob efeito do viés da exclusão de indivíduos nos levantamentos ou representam, de fato, o estágio de maturidade em que as florestas se encontram.

A maioria dos levantamentos utilizaram a altura dos indivíduos como critério de inclusão (Schaeffer-Novelli & Cintrón-Molero 1986). Outros estudos utilizam o diâmetro à altura do peito, pois a distribuição de indivíduos em diferentes classes diamétricas sugere diferenças estruturais associadas ao estágio de desenvolvimento dos bosques. Entretanto, ao utilizar diâmetros diferentes, de 2,5 a 5 cm, os trabalhos podem excluir as menores classes diamétricas, que são representativas para definir o estagio de maturidade das florestas. A maior contribuição em área basal viva na classe diamétrica ≥10 cm é descrita como característica de florestas de mangue maduras com elevado desenvolvimento estrutural (Petri et al. 2011), enquanto que a

alta densidade de troncos nas menores classes diamétricas, menor altura e menor taxa de área basal viva caracterizam bosques menos complexos estruturalmente (Smith 1992).

Quanto à altura, a seleção de indivíduos maiores do que 1.3 m pode descaracterizar regiões que possuem indivíduos de menor porte como característica intrínseca, como as regiões de interior dos bosques e áreas de transição entre manguezal e Floresta de Terras Baixas. Vários estudos suportam essa premissa, mas esta variação não foi encontrada em todos os manguezais (Schaeffer-Novelli et al. 1990; Pellegrini et al. 2000; Estrada et al. 2013).

A importância de fatores ambientais em levantamentos

As interações entre as populações e o ambiente em que estão inseridas podem determinar tanto o padrão espacial quanto temporal na estrutura das florestas (Schaeffer-Novelli et al. 2000; Hogarth & Hogarth 2007). Os manguezais apresentam grande heterogeneidade na estrutura dos bosques, não apenas relacionado com a ocorrência dos indivíduos mas também com as características estruturais e funcionais, como resultado da variação local dos fatores ambientais.

Sete dos 23 estudos levantados abordaram áreas que variaram nas distâncias da costa ou do rio, o que representa um gradiente de dinâmica de inundação, salinidade e/ou evaporação (Lüttge 2008). Neste gradiente, o ambiente é alterado previsivelmente, gerando nichos espaciais diferenciados que refletem no estabelecimento das espécies, por meio da seleção e fixação de propágulos e nos processos ecofisiológicos dos indivíduos (Lüttge 2008; Lima & Tognella 2012).

As diferentes tolerâncias das espécies frente aos fatores abióticos geradas pelo gradiente de inundação tendem a um padrão de zonação: a porção mais próxima do corpo hídrico tende a estar sob influência de processos de origem estuarina, como dinâmica de marés e aporte de água doce, enquanto áreas mais internas estão sujeitas à processos de origem atmosférica, como precipitação, além das variações na topografia (Snedaker 1982; Smith 1992; Lüttge 2008). Entretanto, nem todas as florestas de manguezais apresentam padrões de zonação (Schaeffer-Novelli et al. 1990; Smith 1992; Soares 1999). Apenas três dos levantamentos analisados abordaram a zonação na distribuição das espécies, sendo que, destes, apenas dois realizaram análises quantitativas nos parâmetros ambientais que variaram neste gradiente. A falta de metodologia padronizada impede que os

estudos sejam comparados e extrapolados para a zonação dos demais manguezais próximos.

Qual a melhor abordagem para levantamentos em manguezais?

Os resultados levantados não podem ser extrapolados em escala regional em virtude da variação na escala ambiental abordada e nos detalhes metodológicos, como critério de inclusão e tamanho das parcelas analisadas. Ainda que áreas geograficamente próximas tenham características semelhantes, fatores ambientais que variam em diferentes escalas podem interferir na distribuição das espécies. Os levantamentos analisados sugerem que a composição e o desenvolvimento das florestas de manguezal na costa do Brasil variam em escala local, sendo as características levantadas intrínsecas de cada floresta.

Os estudos atuais associam a ocorrência das espécies à uma variedade de fatores ambientais e bióticos. Porém, a escala de variação destes fatores precisa ser levada em consideração, uma vez que permitirá melhor interpretação dos resultados para subsidiar ações de manejo e conservação. Fatores como salinidade, dinâmica de marés, competição interespecífica e grau de impacto ambiental são apontados como atuantes na configuração atual das florestas de mangue. Apesar da importância destes fatores, apenas quatro dos 23 levantamentos analisados apresentam uma avaliação quantitativa das variáveis ambientais. A falta de dados quantitativos dificulta o estabelecimento das correlações entre estrutura e ambiente, pois os fatores ambientais atuantes são, em sua maioria, covariantes e dependentes entre si. Estudos quantitativos podem ajudar a dissociar os efeitos relativos a cada parâmetro e elucidar os processos que resultaram na estrutura dos manguezais encontrada atualmente.

O próximo passo nas pesquisas sobre a estrutura de manguezais deve focar na funcionalidade dos sistemas. O uso de vários níveis de observação pode revelar a organização ecológica da comunidade arbórea de mangues e permitir a comparação entre os estudos. Investigações que avaliem quantitativamente as características ecofisiológicas das espécies, parâmetros físico-químicos dos ambientes associados à estrutura das florestas e parâmetros em diferentes escalas temporais e espaciais podem auxiliar na interpretação dos processos que ao longo do tempo definiram os padrões estruturais atualmente encontrados.

Os levantamentos existentes parecem ser suficientes para caracterizar a estrutura das comunidades, mas não há resultados satisfatórios sobre os processos

ecológicos que definiram os padrões de distribuição e desenvolvimento das espécies, ao longo do tempo. Portanto, a inclusão de componentes influenciados por características intrínsecas de cada espécie, como tolerância à fatores ambientais e respostas à competição entre indivíduos, pode ser relevante para os padrões estruturais encontrados.

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Tabela 4-1: Levantamentos realizados em florestas de manguezais ao longo da costa brasileira, entre os anos 2000 e 2015.

Referência	Espécies	Critério de Inclusão	Compara áreas?	Aborda variação ambiental?	Relaciona a ocorrência das espécies com quais fatores?
Norte					
Silva & Fernandes, 2004	*A. germinans* *R. mangle*	DAP >3cm	Analisa áreas semelhantes	Sim	Competição
Seixas et al., 2006	*A. germinans* *R. mangle*	DAP >3cm	Analisa áreas semelhantes	Não	Interações bióticas e competição
Matni et al., 2006	*A. germinans* *R. mangle* *L. racemosa*	DAP >2.5cm	Áreas diferem em salinidade e frequência de inundação	Sim	Variações de salinidade e dinâmica de inundação
Nordeste					
Deus et al. 2003	*A. germinans* *R. mangle* *L. racemosa*	DAS >1.5cm	Áreas diferem em salinidade e impacto humano	Sim	Variações de salinidade e grau de conservação
Paraguassu & Silva 2007	*L. racemosa* *R. mangle*	DAP >5cm	Áreas diferem em grau de impacto humano	Não	Impacto humano, como corte seletivo
Soares et al 2008	*A. schaueriana* *R. mangle* *L. racemosa*	Todos indivíduos	Analisa áreas semelhantes	Não	Dinâmica de marés, salinidade e aporte de água doce
(Camargo Maia and Coutinho 2012)	*A. germinans* *A. schaueriana* *R. mangle* *L. racemosa*	Não informado	Áreas diferem em grau de impacto humano	Não	Conteúdo de matéria orgânica no solo e salinidade
Santos et al. 2012	*A. schaueriana* *R. mangle*	Altura >1m	Analisa áreas semelhantes	Sim	Impacto humano

Referência	Espécies	Critério de Inclusão	Compara áreas?	Aborda variação ambiental?	Relaciona a ocorrência das espécies com quais fatores?
Souza & Sampaio 2013	*L. racemosa* *A. germinans* *A. schaueriana* *R. mangle* *L. racemosa*	Todos indivíduos	Áreas diferem em grau de conservação	Sim	Impacto humano e textura do solo
Sudeste					
Soares et al. 2003	*A. germinans* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em grau de impacto humano	Não	Variação espaço-temporal de distúrbios naturais e impacto humano
Silva et al. 2005	*A. germinans* *A. schaueriana* *R. mangle* *L. racemosa*	DAP >2.5cm	Áreas diferem em distância da costa	Sim	Dinâmica de marés e aporte de água doce
Pereira et al 2009	*A. schaueriana* *R. mangle* *L. racemosa*	DAP >5cm	Áreas diferem em grau de impacto humano	Não	Grau de conservação
Bernini & Rezende 2011	*A. germinans* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em distância da costa	Não	Distância de costa e fatores bióticos
Petri et al 2011	*A. germinans* *A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Analisa áreas semelhantes	Não	Condições ambientais diversas
Schmiegelow & Gianesella 2014	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1.3m	Áreas diferem em distância do corpo hídrico principal	Não	Regime de marés, textura do solo e a ausência de déficit de água na região

Referência	Espécies	Critério de Inclusão	Compara áreas?	Aborda variação ambiental?	Relaciona a ocorrência das espécies com quais fatores?
Bernini et al. 2014	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em grau de impacto humano	Sim	Regime de inundação e competição
Mano-Clara & Schmiegelow 2015	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em grau de impacto humano	Não	Impacto humano
Calegario et al. 2015	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em distância do corpo hídrico principal e salinidade	Sim	Conteúdo de matéria orgânica no solo e salinidade
Sul					
Tognella de Rosa et al. 2006	*A. schaueriana* *R. mangle* *L. racemosa*	Todos individuos	Áreas diferem em distância do corpo hídrico principal	Não	Dinâmica de ondas e temperatura
Kilca et al. 2011	*A. schaueriana* *R. mangle* *L. racemosa*	DAP >3m	Analisa áreas semelhantes	Não	Condições ambientais diversas
Oliveira & Tognella 2014	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1.3m	Áreas diferem em distância da costa	Não	Distancia da costa e fatores bióticos
Madi et al (no prelo)	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em grau de impacto humano e distância da costa	Sim	Conteúdo de matéria orgânica no solo e salinidade
Larcher et al (comunicação pessoal)	*A. schaueriana* *R. mangle* *L. racemosa*	Altura >1m	Áreas diferem em distância da costa	Sim	Distância da costa e nutrientes do solo

CONSIDERAÇÕES FINAIS

As três espécies (*A. schaueriana*, *L. racemosa* e *R. mangle*) ocorreram nos manguezais estudados - Baía de Antonina, Baía de Guaratuba e Baía da Babitonga - porém, apresentaram grande variação na densidade, dominância e frequência entre as baías e entre parcelas dentro de cada baía. O número de indivíduos de *R. mangle* e o DAP de *A. schaueriana* e *L. racemosa* foram as variáveis que mais influenciaram na distinção entre baías e entre parcelas dentro de cada estuário. Essas diferenças estruturais podem ser atribuídas às variações em escala local (por exemplo, sedimentação, salinidade e disponibilidade de nutrientes), além da seletividade das espécies aos nutrientes.

Enquanto o padrão de distribuição de *A. schaueriana* nas três baías foi semelhante, no qual a densidade decresceu da borda para o interior do manguezal, *R. mangle* ocorreu em maior densidade em Antonina e *L. racemosa* apresentou maior densidade em Babitonga. A seletividade distinta entre *R. mangle* e *L. racemosa* aos nutrientes do solo - Ca e P - pode explicar o padrão de distribuição dessas espécies nas diferentes baías. Antonina e Babitonga apresentaram valores de salinidade semelhantes, apesar de terem diferido em suas respectivas distâncias da costa.

Todavia, a maior proximidade da costa dos manguezais estudados na Baía de Guaratuba parece ter favorecido o estabelecimento de um gradiente de dinâmica hidrológica ao longo da planície de inundação. Esse padrão parece ter influenciado a concentração de nutrientes e matéria orgânica nas diferentes zonas na planície de inundação. A variação em escala local pode ter influenciado os padrões de estrutura encontrados.

Nos manguezais de Antonina e Babitonga não houve diferenças na salinidade da água intersticial e nos nutrientes do solo ao longo da planície de inundação. Nesses manguezais, não foi observado um padrão de zonação das espécies arbóreas. Entretanto, a zonação observada em manguezais da Baía de Guaratuba foi congruente com as variações de salinidade e textura do solo. Em Guaratuba, *L. racemosa* exibiu maior densidade de indivíduos na borda, enquanto *R. mangle* teve maior densidade nas áreas de interior e *A. schaueriana* exibiu maior dominância na borda, sendo essa última pouco expressiva em áreas de interior.

De modo geral, pouco se sabe sobre os processos que influenciaram a estrutura atual dos manguezais. Entretanto, padrões de zonação podem ser resultado de diferenças ecofisiológicas entre as espécies, as quais proporcionam vantagens competitivas à determinada condição dos manguezais. As diferenças na

ecofisiologia das espécies podem refletir em maior sucesso, por exemplo, por meio do balanço entre incorporação de carbono e perda de água por transpiração. Logo, os resultados do segundo capítulo deste estudo indicaram que, tanto os parâmetros de trocas gasosas quanto a assinatura isotópica, expressaram a maneira pela qual as espécies respondem às mudanças locais de salinidade.

No manguezal de Guaratuba, a taxa fotossintética de *L. racemosa* variou entre parcelas, assim como a condutância estomática em *A. schaueriana* e a transpiração em *R. mangle*. Entretanto, as três espécies apresentaram grande variação entre elas mas pouca variação significativa entre parcelas para a mesma espécie. A *WUEi* e a assinatura isotópica das espécies mostraram que *R. mangle* e *L. racemosa* tiveram uma faixa mais estreita de tolerância à salinidade do que *A. schaueriana*. *Avicennia schaueriana* foi mais tolerante à salinidade devido à sua capacidade para manter a alta *WUEi*, mesmo com grande condutância estomática. Os indivíduos dessa espécie foram dominantes nas áreas de borda, nas quais a salinidade da água intersticial foi maior.

A *WUEi* de indivíduos de *L. racemosa* não diferiu entre as parcelas, entretanto, esses indivíduos apresentaram $\delta^{13}C$ negativamente correlacionado com a salinidade da água intersticial, sugerindo alta eficiência no uso da água a longo prazo. As correlações entre trocas gasosas e características do solo para *L. racemosa* indicaram que a salinidade da água intersticial e o pH do solo afetaram a distribuição dos indivíduos ao longo da planície de inundação, provavelmente por influenciar na sua capacidade fotossintética.

Nos indivíduos de *R. mangle,* os parâmetros de trocas gasosas foram pouco correlacionados com as variáveis de solo estudadas, sugerindo que outros fatores podem ter interferido na sua distribuição. Fatores como diferenças na tolerância às variações na salinidade, sobrevivência de propágulos e interações bióticas parecem relacionados com a ocorrência de *R. mangle*.

Os resultados desse estudo nas Baías de Antonina, Babitonga e Guaratuba demonstraram a importância da variação ambiental em escala local na estrutura das florestas. De fato, padrões de distribuição das espécies de mangue foram relatados desde os primeiros estudos ecossistêmicos. Porém, ainda que diversos padrões estruturais já tenham sido caracterizados, não existem resultados satisfatórios sobre os processos ecológicos que influenciaram a estruturação dessas florestas ao longo do tempo.

Levantamentos fitossociológicos realizados entre os anos de 2000 e 2015, sugeriram estruturas florestais distintas ao longo da costa brasileira. Apesar de não

serem comparáveis, os levantamentos indicam a influência de atividades antrópicas sobre a estrutura das florestas analisadas.

Os levantamentos fitossociológicos compilados nesse estudo divergiram na metodologia adotada, o que dificulta a comparação de resultados e a definição acurada da relação estrutura/desenvolvimento/variáveis ambientais. A falta de metodologia comparável também impediu que os resultados disponíveis a respeito da estrutura dos manguezais brasileiros sejam extrapolados. Da mesma maneira, a carência de dados quantitativos dificulta o estabelecimento das correlações entre estrutura e variação ambiental, pois torna-se difícil dissociar os efeitos de fatores ambientais que são dependentes entre si, tais como composição do solo, frequência de inundação e salinidade.

Nesse estudo, a ecologia dos manguezais foi abordada em diferentes escalas, porém, ainda existem lacunas no entendimento dos processos ecológicos peculiares desse ambiente. Investigações que avaliem quantitativamente as características ecofisiológicas das espécies, parâmetros físico-químicos dos ambientes associados à estrutura das florestas e parâmetros em diferentes escalas temporais e espaciais podem auxiliar na interpretação dos processos que ao longo do tempo definiram os padrões estruturais observados no presente. Elucidar esses processos pode auxiliar na elaboração de projetos de manejo e instrumentos legais para a conservação das áreas de manguezais.

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SUPPLEMENTARY DATA

Table S1: Mean values (± standard deviation) of soil attributes of the Antonina Bay mangrove forests, by zones and divided into two depths. K: Potassium content ($mmol_c.dm^{-3}$), Mg: Magnesium content ($mmol_c.dm^{-3}$), Na: Sodium content ($mmol_c.dm^{-3}$), H+Al: Aluminum saturation ($mmol_c.dm^{-3}$), CEC: Cation Exchange Capacity ($mmol_c.dm^{-3}$), B: Boron content ($mg.dm^{-3}$), Cu: Copper content ($mg.dm^{-3}$), Fe: Iron content ($mg.dm^{-3}$), Mn: Manganese content ($mg.dm^{-3}$), Zn: Zinc content ($mg.dm^{-3}$).

	Zone	K	Mg	Na	H + Al	CEC	B	Cu	Fe	Mn	Zn
10 cm deep	Fringe	15.5 ±7.1	59.2 ±22.4	329.7 ±43.0	69.8 ±30.1	200.0 ±37.5	12.8 ±5.9	0.8 ±0.6	276.5 ±24.5	14.7 ±3.4	2.5 ±1.9
	Intermediary	7.3 ±1.3	39.6 ±34.3	264.4 ±68.1	112.2 ±42.3	210.7 ±15.6	15.4 ±6.8	0.3 ±0.3	315.4 ±24.6	8.7 ±3.8	1.9 ±0.8
	Interior	7.6 ±0.5	16.8 ±11.0	278.1 ±24.6	59.3 ±14.5	132.6 ±26.4	13.7 ±3.2	0.6 ±0.2	284.3 ±15.9	5.4 ±0.9	3.7 ±0.4
30 cm deep	Fringe	17.1 ±9.6	43.2 ±24.8	294.3 ±39.9	105.3 ±39.3	226.9 ±33.5	15.2 ±2.5	0.3 ±0.3	288.3 ±39.4	13.4±2.8	1.4 ±0.4
	Intermediary	7.5 ±1.0	21.0 ±13.2	268.6 ±70.8	117.8 ±39.6	196.5 ±53.3	16.0 ±3.5	1.6 ±3.6	328.6 ±8.4	7.3 ±4.8	3.8 ±5.6
	Transition	7.7 ±0.9	24.3 ±14.3	263.0 ±62.4	75.0 ±15.8	161.7 ±27.6	14.2 ±1.7	0.5 ±0.6	306.3 ±22.5	5.0 ±3.2	3.3 ±2.3

Table S2: Mean values (± standard deviation) of soil attributes of the Guaratuba Bay mangrove forests, by zones and divided into two depths. K: Potassium content ($mmol_c.dm^{-3}$), Mg: Magnesium content ($mmol_c.dm^{-3}$), Na: Sodium content ($mmol_c.dm^{-3}$), H+Al: Aluminum saturation ($mmol_c.dm^{-3}$), CEC: Cation Exchange Capacity ($mmol_c.dm^{-3}$), B: Boron content ($mg.dm^{-3}$), Cu: Copper content ($mg.dm^{-3}$), Fe: Iron content ($mg.dm^{-3}$), Mn: Manganese content ($mg.dm^{-3}$), Zn: Zinc content ($mg.dm^{-3}$).

	Zone	K	Mg	Na	H + Al	CEC	B	Cu	Fe	Mn	Zn
10 cm deep	Fringe	8.4 ±1.8	36.0 ±34.2	235.8 ±77.1	70.4 ±66.9	168.4 ±67.7	16.6 ±4.1	0.3 ±0.3	168.2 ±105.0	6.1 ±4.2	2.3 ±0.9
	Intermediary	7.6 ±0.9	48.0 ±36.9	168.4 ±22.2	42.5 ±25.0	137.6 ±31.2	18.1 ±7.7	0.3 ±0.2	147.8 ±111.0	3.5 ±3.5	2.1 ±2.4
	Interior	7.8 ±1.1	37.5 ±38.8	193.9 ±44.2	45.0 ±12.5	138.6 ±46.2	17.0 ±6.5	0.4 ±0.1	137.0 ±85.1	3.1 ±2.6	1.8 ±0.9
30 cm deep	Fringe	7.3 ±2.7	31.0 ±34.3	230.7 ±106.3	78.6 ±20.0	159.7 ±40.5	21.5 ±3.3	0.2 ±0.2	176.8 ±128.9	4.4 ±3.7	2.3 ±1.8
	Intermediary	7.0 ±1.0	78.5 ±37.9	183.5 ±28.6	56.3 ±14.1	184.2 ±30.1	17.0 ±3.4	0.4 ±0.1	205.0 ±142.5	4.3 ±2.6	2.5 ±1.6
	Interior	7.1 ±1.4	59.5 ±34.9	182.7 ±21.5	41.0 ±14.1	152.8 ±21.5	19.9 ±2.1	0.5 ±0.1	225.0 ±94.9	3.7 ±1.9	1.9 ±1.1

Table S3: Mean values (± standard deviation) of soil attributes of the Babitonga Bay mangrove forests, by zones and divided into two depths. K: Potassium content ($mmol_c.dm^{-3}$), Mg: Magnesium content ($mmol_c.dm^{-3}$), Na: Sodium content ($mmol_c.dm^{-3}$), H+Al: Aluminum saturation ($mmol_c.dm^{-3}$), CEC: Cation Exchange Capacity ($mmol_c.dm^{-3}$), B: Boron content ($mg.dm^{-3}$), Cu: Copper content ($mg.dm^{-3}$), Fe: Iron content ($mg.dm^{-3}$), Mn: Manganese content ($mg.dm^{-3}$), Zn: Zinc content ($mg.dm^{-3}$).

	Zone	K	Mg	Na	H + Al	CEC	B	Cu	Fe	Mn	Zn
10 cm deep	Fringe	7.6 ±2.6	38.8 ±22.4	216.1 ±86.1	62.5 ±28.0	159.3 ±46.1	15.3 ±5.4	0.8 ±0.5	236.7 ±83.3	6.7 ±4.0	6.3 ±3.2
	Intermediary	8.1 ±2.4	20.0 ±14.7	240.3 ±47.5	68.4 ±32.9	153.7 ±52.4	16.9 ±4.8	0.6 ±0.4	260.0 ±44.9	7.6 ±2.8	5.1 ±2.3
	Interior	5.9 ±1.0	41.3 ±32.1	258.2 ±52.2	129.3 ±90.9	237.4 ±63.3	16.5 ±6.3	0.3 ±0.3	267.5 ±43.1	4.3 ±2.0	3.4 ±1.8
30 cm deep	Fringe	7.1 ±1.0	21.5 ±16.1	235.2 ±64.3	88.0 ±31.4	182.1 ±36.2	19.5 ±6.2	0.3 ±0.2	278.3 ±54.0	4.9 ±3.0	3.5 ±1.4
	Intermediary	6.8 ±1.9	31.8 ±20.9	249.2 ±84.1	65.8 ±26.1	161.0 ±19.1	16.0 ±6.6	0.4 ±0.2	239.2 ±70.6	4.2 ±2.1	4.0 ±2.3
	Transition	6.0 ±1.2	50.8 ±44.5	227.2 ±57.8	81.8 ±34.1	183.0 ±34.9	13.5 ±1.7	0.3 ±0.3	287.8 ±54.6	4.9 ±2.1	4.2 ±1.7